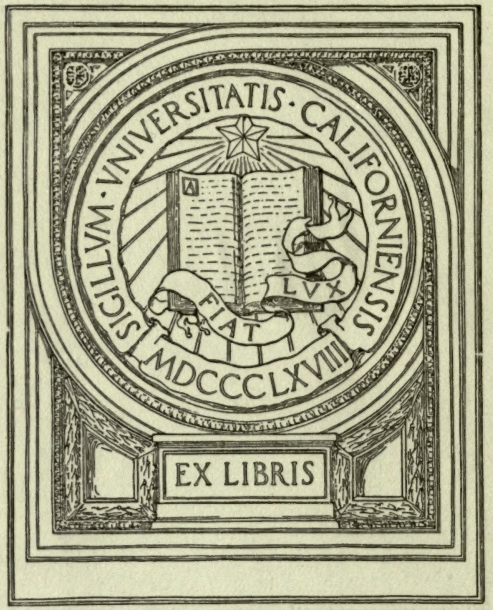

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MANUAL OF PALÆONTOLOGY

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MANUAL OF PALÆONTOLOGY

FOR THE USE OF STUDENTS

WITH A GENERAL INTRODUCTION ON THE PRINCIPLES OF PALÆONTOLOGY

BY

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ADDENDA ET CORRIGENDA TO PART III.

Page 901, line 13 from bottom, *for* "Weinsheimer" *read* "Wiedersheim."

" 912, line 2 from top, *for* "Teleotomi" *read* "Teleostomi."

" 928, line 17 from top, *for* "*Hypocladodus*" *read* "*Hybocladodus.*"

" 928, line 8 from bottom, *for* "*Scilliidæ*" *read* "*Scylliidæ.*"

" 944. *Carcharopsis* is identical with *Dicrenodus* (p. 928).

" 945, line 6 from bottom, *before* "no basal" *add* "usually."

" 951. *Myriacanthus* has recently been made the type of a distinct family—the *Myriacanthidæ* (see Appendix).

" 955. *Ceratodus* has recently been recorded from the Stormberg beds of the Karoo system of S. Africa.

" 965. *Pnigeacanthus* is identified with *Oracanthus* (p. 947).

" 966, line 11 from top, *before* "very minute" *add* "usually."

" 966, line 5 from bottom, *dele* "minute."

" 967, line 4 from top, *for* "Carboniferous" *read* "Devonian."

" 969, line 9 from top, *dele* "and Carboniferous."

" 971, fig. 905, *for* "*Heberti*" *read* "*Hibberti.*"

" 978. *Palæoniscus* occurs in the Stormberg beds of the Karoo system of S. Africa; and from the underlying Beaufort beds a fish allied to *Rhabdolepis* has lately been described as *Atherstonia.*

" 979. The name "*Platysomidæ*" should be amended to "*Platysomatidæ.*"

" 988, line 22 from bottom, *dele* "as in *Belonorhynchus.*" The genus *Belonorhynchus* has recently been described from the Australian Hawkesbury beds; while *Belonostomus*, or a closely allied form, is recorded from the Lameta Cretaceous of India.

" 989. *Hypsicormus* has been recently described from the Oxford Clay, and *Eurycormus* from the Kimeridge Clay of England.

" 1004, line 20 from bottom, *for* "*Saurinichthys*" read "*Taurinichthys.*"

" 1033. A species of *Bothriceps* has been recently recorded from the Karoo system of S. Africa.

Page 1035. The name *Platyops* being preoccupied, may be changed to *Platyoposaurus*. The genus should apparently be included in the *Archegosauridæ*, since the vertebræ are described as rhachitomous.

" 1036. *Capitosaurus* also occurs in the Bunter. The superiority of size of *Capitosaurus* over *Trematosaurus* renders it more probable that the former is the same as *Chirosaurus* (p. 1039).

" 1036, 1037. The alleged occurrence of *Mastodonsaurus giganteus* and *Metopias* in the Rhætic rests on insufficient evidence. The latter genus is stated to have been recorded from the Continental instead of the British Rhætic.

" 1041, bottom line, *dele* " and may not improbably be identical with *Chelotriton*."

" 1043, line 8 from top, *for* " each " *read* " hind," *and for* " pes " *read* " same." *Alytes* occurs in the Miocene of Sausan (*Rana Troscheli*). *Latonia* (p. 1044), according to Cope, is not allied to *Ceratophrys*, but belongs to the *Discoglossidæ;* it also occurs in the Sausan Miocene. The *Palæobatrachidæ* appear to connect the *Pelobatidæ* with the Aglossa, as represented by the *Dactylethridæ*, or *Xenopodidæ* as they should properly be called,—*Dactylethra* being a synonym of *Xenopus*.

" 1044. The name *Cystignathidæ* should be replaced by *Leptodactylidæ*, *Cystignathus* being a synonym.

" 1057, line 8 from top, *before* " characterised " *add* " typically."

" 1057, line 17 from top, *before* " African " *add* " typical."

" 1058-61. Additional characters of many of the genera are given in the Appendix.

" 1059, line 4 from top, *for* " divided " *read* " undivided."

" 1059, line 7 from top, *for* " single " *read* " double."

" 1108. *Ocadia* is distinct from *Palæochelys*. See Appendix.

" 1117, line 10 from bottom, the name " *Cyclanorbinæ* " may be substituted for " *Emydinæ*," since the latter is preoccupied.

" 1126. Since *Ichthyosaurus platyodon* differs from all other species of *Ichthyosaurus* by the smooth and carinated crowns of its teeth (fig. 1028), it appears, on the whole, advisable to regard it as the type of a distinct genus, for which the name *Temnodontosaurus* is proposed.

" 1139. *Rhaphiosaurus* proves to be founded upon part of a jaw of *Pachyrhizodus* (p. 993).

" 1176, line 2 from top, *for* " Kimeridgian " *read* " Portlandian."

" 1179, line 18 from top, *after* " species " *add* " of the former."

" 1264, fig. 1130. A is a skull of *Manis*, and not *Echidna*, as stated.

" 1372, lines 16, 17, from top, *for* "*Limnotherium*" *read* "*Limnohyus*."

PART III.

PALÆOZOOLOGY

VERTEBRATA

BY

R. LYDEKKER

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PART III.

CHAPTER XLV.

SUB-KINGDOM VERTEBRATA.

General Characters.

The Vertebrata, or highest types of the entire animal kingdom, are distinguished as a whole from all the preceding sub-kingdoms (collectively designated as the Invertebrata) by the general presence of an internal skeleton, and more especially of a cylindrical longitudinal axis, termed the notochord, which is usually replaced in the adult by a series of cartilaginous or bony segments collectively constituting the *vertebral column*. This axis, or column, separates the smaller dorsal or neural tube of the body from the larger ventral or visceral (hæmal) tube; and the body itself, together with its appendages, is always symmetrical to this axis, and is never externally divided into segments. Limbs may be completely wanting, but when present they never exceed two pairs, and are always turned away from the dorsal or neural aspect of the body.

That the Vertebrata have been derived from the Invertebrata at an extremely early epoch of the earth's history is practically certain; and, although we are unable to point to the direct ancestors of the sub-kingdom, yet we have an inkling of this relationship exhibited by the presence of a notochordal structure in the earlier stages of the Ascidians, while there are also certain features in the organisation of the Annelids suggestive of their being allied to the primitive stock whence the Vertebrates took their origin. Since, however, it is probable that these primitive types were soft animals, it is unlikely that any light will be thrown on the origin of Vertebrates by means of Palæontology; and if the problem is ever to be solved it will be by the aid of Embryology.

Leaving then the origin of Vertebrates as an unsolved problem, in the solution of which the palæontologist can have but little share, we may proceed to a brief survey of the classification and chief structural features of the Vertebrate sub-kingdom, so far as they concern the palæontologist.

For this purpose the sub-kingdom may be divided into five classes[1]—viz., Pisces or Fishes, Amphibia or Amphibians, Reptilia or Reptiles, Aves or Birds, and Mammalia or Mammals—of which some of the more important features, from the point of view of the palæontologist, will be mentioned under these respective heads.

The first and second classes have been brigaded together by Professor Huxley under the name of Ichthyopsida, and the third and fourth as Sauropsida; and these terms will frequently be found convenient. Other writers, again, from the absence or presence of certain structures during the course of development, group together the two first classes as Anamniota (Anallantoidea, or Branchiata), and the remaining three as Amniota (Allantoidea, or Abranchiata).

Since the hard parts of Vertebrates are those with which alone the student of Palæontology usually has to deal, it will generally be unnecessary in this work to make any allusion to the soft parts of the body. With, regard, however, to these hard portions, it is advisable to give an extremely brief sketch of the more important elements of the Vertebrate *endo-* and *exoskeleton* for the benefit of those readers who are unacquainted with the elements of Comparative Osteology. It must, however, be distinctly understood by all who desire to practically study the history and structure of extinct Vertebrates, that it is absolutely essential they should have that thorough knowledge of the osteology of the recent members of the sub-kingdom which can only be gained by familiarity with actual specimens, accompanied by patient and laborious study of the numerous works on the subject. The following sketch is, indeed, merely sufficient to enable the reader to understand the meaning of the terms employed in the sequel; and throughout the Vertebrata the limits of this work will necessarily permit of only some of the more salient features of the skeleton of the various groups being mentioned. It may also be observed that those groups which have wholly disappeared, or of which the palæontological and evolutionary history is of especial interest, are more fully treated of than those more or less exclusively confined to the later or present epochs, and of which the history is fully recorded in those works to which the term "Natural History" is usually restricted. In the majority of instances, again, space does not permit of allusion to species; but

[1] A sixth class — Leptocardii — is formed for the reception of the Lancelet (*Amphioxus*), with which the palæontologist has, unfortunately, no concern, as its past history is a blank.

in the case of very large genera, where the species differ considerably in essential characters, attention is in some instances directed to the more important specific types. The student must not, moreover, expect to find that every known genus of fossil Vertebrates, or even every family, is mentioned in the following chapters, of which the object is to enable him to gain a fair general knowledge of the past history, distribution, and leading structural features of the best known groups of the various classes.

Commencing with the outer skeleton or *exoskeleton* it may be observed that, as a rule, the palæontologist has but little to do with structures developed in the *epidermis*, or layer overlying the true skin or *dermis*, since these generally perish during the process of petrifaction. The scales of Lizards belong, however, to this layer, and their impressions are in some instances preserved; while in the Chelonia the boundaries of the horny shields, covering the bony shell, are in some instances the most important characters by which fossil specimens can be determined. Occasionally, again, as in the Solenhofen *Archæopteryx*, the feathers of Birds have left their impression in rocks of which the material is of a fine-grained structure; while still more rarely, as in the bony covering of some Glyptodonts, pits from which hairs or bristles once grew are preserved in a fossil state.

The *dermal* exoskeletal structures are of considerably more importance from a palæontological point of view; and it should be observed that in nearly all the classes there appears to have been a gradual tendency to the disappearance of the bony elements of this skeleton in the higher forms, this being especially marked in the case of Fishes. In the latter class the scales of all types, of which fuller mention will be made in the sequel, belong to the dermis, and in some forms there may be a complete dermal armour formed of imbricating scutes, as in *Callichthys* among the Siluroids, or, as in the Coffer-fishes (*Ostracion*), consisting of calcified scutes with their edges in apposition. Apparently the most primitive type of dermal armour in this class consists of small denticules supported on bony plates, and it has been found that such denticules are absolutely homologous with true teeth, of which we shall speak presently. The bony *fin-rays*[1] and *fin-spines* of Fishes are another development of the dermal skeleton, which will be noticed under the head of that class; although it may be observed here that many of the latter are closely allied in structure to teeth. Again, the dermal skeleton in many extinct Amphibians and Reptiles takes the form of a more or less complete armour, either on the ventral or the dorsal, and not unfrequently on both aspects of the body, con-

[1] These dermal fin-rays must not be confounded with the radial cartilages of the endoskeleton.

structed of solid bony *scutes*, which may imbricate or overlap one another, like the tiles on a roof, or may be firmly united at their edges by sutural union. Such an armour may also develop enormous bony spines, often attached to the skin by an expanded base which represents the scutes. In the latter class, again, the bony shells of the Testudinate Chelonia are formed partly of dermal elements, blended with others belonging to the endoskeleton to form a continuous whole; while in the Athecate division of the same order the whole of the protective armour is of dermal origin.

The so-called membrane bones of the skull, and the clavicular portions of the pectoral girdle, are likewise of dermal origin, and therefore properly belong to the exoskeleton; but their intimate connection with cartilage bones renders it more convenient to consider them with the endoskeleton.

Teeth, as belonging to the list of dermal structures, may be conveniently noticed here; and the importance of these organs to the palæontologist can scarcely be overrated, since from their extreme density they are more often preserved in a perfect condition than most other parts of the skeleton, and thus frequently form the only safe guide to the affinities of an extinct type. Teeth are composed of two or more earthy constituents, varying in their structure, and the amount of animal matter contained in them. The most important element is that known as *dentine* (fig. 813, *d*), which forms the greater portion of the body of most teeth, and consists structurally of extremely minute tubes, cells, and earthy particles. Some dentine is devoid of blood-vessels; but in other cases it is permeated by the latter, when it is known as *vascular*, or *vaso-dentine;* and both these structures may exist in a single tooth. In young teeth (fig. 813) the centre of the dentine mass is occupied by the vascular *pulp-cavity* (*pc*), which is open at the base; but in the adult this cavity is often totally obliterated, by the formation of what is known as *osteo-dentine*, which is a kind of vascular dentine passing imperceptibly into the structure of true bone. The second primary constituent is the *enamel* (*c*), which, when present, immediately overlies the dentine of the *crown*, or exposed portion of the tooth, and is the hardest known animal substance; it is composed of extremely minute prismatic fibres, generally running at right angles to the outer surface of the tooth. This substance is the least constant element in teeth, although it is very generally present in those of Mammals; among the Reptiles it is entirely wanting in the Ophidian Squamata, but is present in the Crocodilia. The

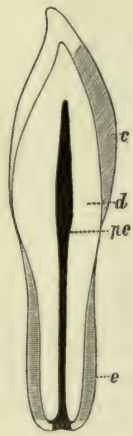

Fig. 813.—Diagrammatic vertical section of a tooth. *e*, Cement; *d*, Dentine; *c*, Enamel; *pc*, Pulp-cavity.

third constituent, usually known as *cement* (fig. 813, *e*), but occasionally as *crusta petrosa*, is the most external of the three: in some instances, as in fig. 813, it is confined to the *root*, or embedded portion of the tooth, where it consequently comes into immediate contact with the dentine; but in other cases it is found overlying the enamel of the crown, and in others again, where the enamel is wanting, it forms the main covering of the crown, as in the teeth of the Edentate Mammals. The cement is always traversed by vascular canals; and its structure is very similar to that of bone, although only occasionally presenting all the peculiarities of the latter.

True teeth are generally confined to the mouth and pharynx, but they may be situated on many of the bones of the former, and their mode of attachment varies from a simple anchylosis to the underlying bone, to implantation in distinct sockets. The simplest forms of teeth are small granular bodies, like the minute ossifications already mentioned as occurring in the skin of certain Fishes; while those of the most complex structure are to be found in certain Fishes (*Dendrodus*), in the Labyrinthodont Amphibians, and among Mammals in the Edentate genus *Orycteropus* and many Rodents and Ungulates. Except in forms where all are alike, as a general rule the teeth at the anterior extremity of the jaws are more or less simple, while there is a gradual increase in their complexity towards the opposite end, and in most cases the lower teeth are narrower and more elongated in an antero-posterior direction than the upper ones.

The importance of teeth to the palæontologist as a means of determining the affinities of fossil forms has been already mentioned; but in many cases their evidence must be supplemented either by that of other remains, or of the geological horizon whence they were obtained; since otherwise serious error may result. Thus, the teeth of the Dinosaurian *Megalosaurus* present a strong resemblance to some of those of the Mammalian *Machærodus;* while the front teeth of some Sparoid Fish approximate to those of the Primates; and the lower hinder teeth of the Kangaroos, of the Dinothere among the Proboscidea, and of the Tapir-like animals in the Perissodactyla, are all singularly alike in form. Another fertile source of error to be guarded against is the great difference in the form of the teeth from different regions of the mouth.

For the microscopic structure of teeth and their mode of development, the student must refer to other works; but a large number of the more important types of dental structure will be found noticed in the course of the following pages.

By far the greater number of adult Vertebrates possess a solid inner, or *endoskeleton*, composed of bone (into the nature of which

it will be unnecessary to enter here); but in others this skeleton remains cartilaginous throughout life, or, as in many Sharks, has solid structures formed by calcifications in the cartilage, which are quite distinct from true bone. This endoskeleton may be divided into an *axial portion*, or that of the head, trunk, and tail; and an *appendicular portion* supporting the limbs; the relations of the two being shown in fig. 814. The anterior part of the axial skeleton is formed by the *skull* (of which we shall speak later); and this is succeeded posteriorly by the *vertebral column*, typically composed of a number of segments, known as *vertebræ*, placed in the middle line of the dorsal side of the body, and continuing from the head to the extremity of the tail. This column is developed round a rod-like axis known as the *notochord*. In certain of the lower forms the latter may persist throughout life, and may either simply have a fibrous or cartilaginous sheath, or may have calcifications, or cartilages, in either the dorsal or ventral portion; and there is a complete transition from such a primitive type of column to that of the more specialised types in which the vertebræ are fully ossified. There is an enormous amount of variation in the structure of the vertebræ of different groups, and even in the different regions of the body of a single animal, but there is one general plan pervading them all. Thus a typical vertebra (fig. 815) consists of a basal portion, or *centrum*, which may be either disk-like or more or less elongated. Its posterior

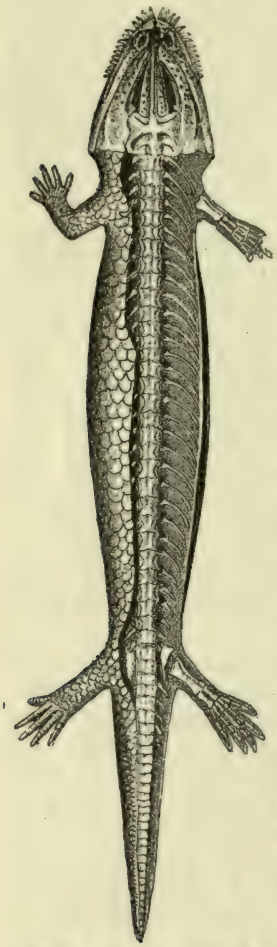

Fig. 814.—Under surface of a Labyrinthodont Amphibian (*Seeleya*), with the dermal armour removed from the left side in order to show the endoskeleton. Greatly enlarged. (After Fritsch.)

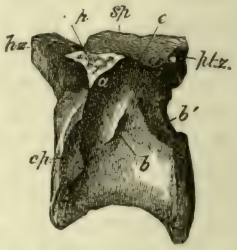

Fig. 815.—Left lateral view of an imperfect amphicœlous dorsal vertebra of a Dicynodont Reptile. *sp*, Neural spine (broken); *pz*, Prezygapophysis; *ptz*, Postzygapophysis; *tp*, Transverse process (broken); *cp*, *Rib*-facet on the centrum; *b*, *b'*, Muscular ridges.

and anterior surfaces, by which (with the intervention of cartilages) it articulates with the adjacent centra, may be nearly flat or concave, when it is said to be *amphicœlous* (fig. 815); or its anterior surface may be more or less hollow, and the posterior convex (fig. 816), when it is termed *procœlous;* or, lastly, the reverse of the latter arrangement may obtain, when the centrum is termed *opisthocœlous;* an example of the latter structure being shown in the vertebra of *Calamospondylus* given in the sequel (fig. 1071). Immediately above the centrum is the aperture of the channel for the reception of the spinal cord, known as the *neural canal* (fig. 816); this canal being enclosed laterally and superiorly by the *neural arches*, which are surmounted by the *neural spine* (figs. 815, 816). The lateral portions of this arch are termed the *pedicles* (fig. 817, *n*), and the parts connecting the latter with the spine the *laminæ*. The arch, it should be observed, always ossifies separately from the centrum, and the line of junction between the two when, as in many Rep-

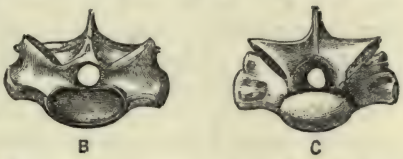

Fig. 816.—Anterior (B) and posterior (C) views of a procœlous dorsal vertebra of a Lacertian Reptile (*Varanus*). The part above B and C is the centrum; the aperture the neural canal, above and round which are the neural arches, surmounted by the neural spine; the oblique facets are the zygapophyses, and the lateral prominences the transverse processes, which are here very short.

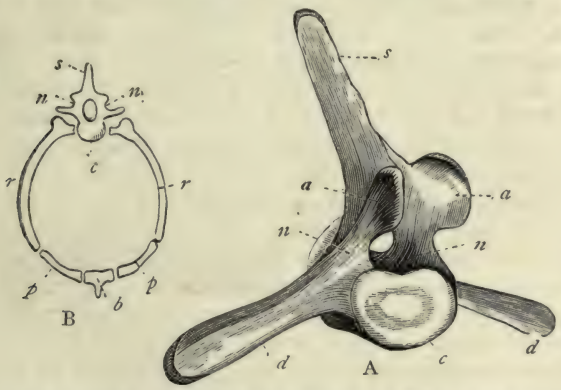

Fig. 817.—A, Oblique anterior view of the lumbar vertebra of a Whale. B, Diagrammatic transverse section of the bones of the thoracic region of a Mammal. Greatly reduced. *a*, Prezygapophyses; *b*, Sternum; *c*, Centrum; *d*, Transverse process; *n*, Pedicle of arch; *p*, Sternal rib; *r*, Rib; *s*, Neural spine. (After Owen.)

tiles, they remain distinct, is known as the *neuro-central suture*. The neural arch bears a pair of processes, or facets, at either extremity for articulation with the adjacent vertebræ; those at the anterior extremity (fig. 816, B) being known as *prezygapophyses*, and

looking inwards and upwards; while those at the other extremity (fig. 816, c) are termed *postzygapophyses*, and look downwards and outwards.[1] Besides these processes for mutual articulation, there are other processes on many vertebræ; the most constant being the *transverse processes*, or *diapophyses*, which may be very short as in fig. 816, or greatly elongated as in fig. 817, A, *d*. These transverse processes may arise either from the arch or from the centrum, and in the trunk frequently serve for the main attachment of the *ribs* (fig. 817, B). In fig. 816 we have an example of a vertebra with very short transverse processes placed mainly on the centrum, while in the vertebra of *Iguanodon*, figured in the sequel (fig. 1058), we see very large transverse processes arising solely from the arch.

The sides of the centrum in the anterior region of the body frequently carry other articular processes for the ribs, which may be termed rib or costal facets (fig. 815, *cp*), or *parapophyses*. Again, the inferior or hæmal surface of a vertebra may bear a *hæmal spine*—the term hæmal being applied to the inferior aspect on account of its being directed towards the heart and large blood-vessels. Each vertebral centrum carries its own arch; but between the true centra of the Ichthyopsida there may be intercalated centra-like bodies, carrying no arches, and termed *intercentra*. Rudiments of such intercentra occur in the so-called *wedge-bones* or *hæmapophyses*, found between the lower borders of the centra in certain Reptiles, and more especially between the first and second vertebræ. Further, the Y-shaped *chevron-bones*, usually articulating between adjacent vertebral centra in the tail of many Vertebrates, are also morphologically intercentral elements. In Fishes the vertebral column can only be divided into *trunk* and *caudal* regions; but in the majority of higher forms further divisions can be made. Thus the vertebræ of the neck, in which the ribs never articulate with the sternum, are termed *cervical* (fig. 818, *c*); the first of this series being designated the *atlas*, and the second the *axis*. It is further remarkable that in most instances the centrum of the atlas is not joined to its arch, but either remains as a distinct element, or becomes anchylosed to the front of the centrum of the axis to form the so-called *odontoid process*; and it appears that in the latter case the inferior bar connecting the two lateral arches of the atlas is really the remnant of the first intercentrum. It is, moreover, probable that this separation of the component elements of the atlas should be regarded as a retention of the primitive feature obtaining in the vertebral column of many extinct Fishes and Amphibians, where, as will be noticed below, the whole of the vertebræ are thus disintegrated. Finally, it has been suggested that certain bony

[1] These are well seen in the vertebra of *Calamospondylus* above mentioned.

splints overlying the arch of the atlas in Crocodiles represent a vertebra intercalated between the latter and the cranium, for which the name *proatlas* has been proposed. It is, however, by no means proved that these splints do not belong to the atlas vertebra, so that an authority like Mr Hulke is disposed to doubt the validity of this alleged additional vertebral segment.

In such Vertebrates as have the hind limbs well developed, one or more of the vertebræ in the hinder part of the trunk differs from the rest, and forms a *sacrum* (fig. 818, *s*), which articulates by anchylosed ribs with the pelvic girdle. The vertebræ forming the region between the sacrum and the last cervical vertebræ in the higher forms consist posteriorly of a *lumbar* series (fig. 818, *l*),

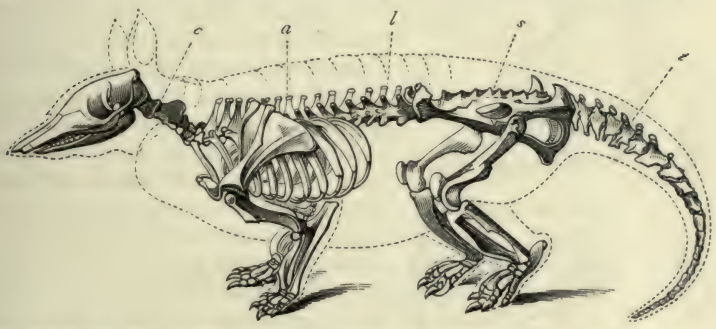

Fig. 818.—Skeleton of an Armadillo, showing the regions of the vertebral column. *c*, Cervical; *d*, Dorsal; *l*, Lumbar; *s*, Sacral; *t*, Caudal region or tail. The pectoral girdle is below *d*, and the pelvic below *s*. Reduced.

without or with very short ribs, and anteriorly of a *dorsal* series (fig. 818, *d*), provided with long ribs, of which the anterior ones articulate with the breast-bone or *sternum*. In many Amphibians, however, in which (as in many Reptiles) there is no sternum, the ribs continue throughout the lumbar and some of the caudal series, as in fig. 814, so that no distinction can be drawn between dorsals and lumbars, and the series between the cervicals and sacrals is consequently called *dorso-lumbar*. The term *caudal* is applied to all those vertebræ posterior to the sacrum. Moreover, where there is no sternum, it is frequently difficult to draw an exact demarcation between cervical and dorsal vertebræ, and we are compelled to rely on analogies drawn from the mode of articulation of the ribs.

Ribs, which have been already mentioned, are nearly always present in the dorsal region, and may occur throughout the length of the vertebral column. According to the views of Dr Baur, they are to be regarded as originally intervertebral structures, since they are attached in some of the earlier forms to the vertebral inter-

centra; but by the disappearance of the latter they have frequently become transferred to the centra or their appendages, although in other cases their original derivation is indicated by their articulation at the junction of two vertebræ. Very generally ribs articulate with the vertebral column by two distinct heads, which is probably the original primitive type of structure. In these cases the anterior or lower head is termed the *capitular*, and articulates with the rib-facet or parapophysis on the vertebral centrum (fig. 815, *cp*); while the posterior or upper head is known as the *tubercular*, and in the dorsal vertebræ articulates with the transverse process or diapophysis of the arch. In the dorsal ribs the two heads may, however, coalesce, and articulate with a facet on the centrum, or with a longer or shorter transverse process on the arch. Frequently, moreover, while the anterior dorsal ribs have double heads, the posterior ones have but a single head articulating with the transverse process. In the caudal region of many Reptiles true ribs articulate with the upper part of the centrum, and except as being separate, are indistinguishable from the caudal transverse processes of many Mammals, such as the Cetacea (fig. 817). Cervical ribs are present in most Reptiles, and usually articulate by two heads to the vertebræ — the upper head joining a facet, generally placed on the arch, corresponding to the transverse process of the dorsal vertebræ, and the lower one articulating to another facet on the centrum. Very rarely in Reptiles these cervical ribs may be completely anchylosed to the vertebræ, as in the vertebra of *Calamospondylus*, figured in the sequel (fig. 1071); and this suggests that at least a portion of the so-called transverse processes of the cervical vertebræ of Mammals, which arise from the vertebræ by double pedicles, really correspond to cervical ribs. In the Sauropterygia both heads of the cervical ribs articulate with the centrum.

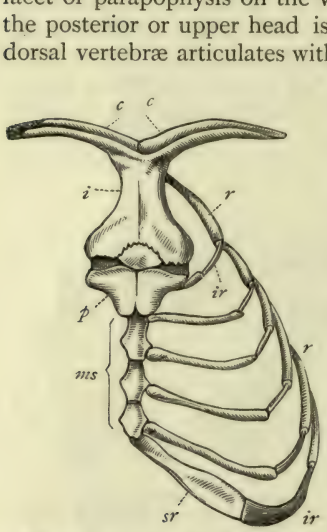

Fig. 819.—Sternal region of a young *Ornithorhynchus*. *c*, Clavicle; *i*, Interclavicle; *p*, Presternum; *ms*, Mesosternum; *r*, Rib; *ir*, Intermediate rib; *sr*, Sternal rib. (After Flower.)

When a sternum is present the distal ends of the dorsal ribs are generally unossified, and are sometimes termed *intermediate ribs* (*ir*, fig. 819); and these unossified elements unite distally with the sternal ribs (*sr*), which in their turn join the sternum (fig. 817, B, *b*). Further, among the Sauropsida lateral ossifications may be developed

on the ribs, termed *uncinate processes*, of which the position is shown in the figure of the skeleton of the Eagle given below (fig. 1106).

The breast-bone or *sternum* (figs. 817, 819) is usually composed of a median series of bones or cartilages on the ventral aspect of the body, which is divisible in the higher groups into an anterior *presternum*, usually consisting of a single ossification; and of a series of *mesosternal* elements, followed posteriorly by the *xiphisternum*. In many Sauropsida the sternal bones have long lateral processes; and the ossifications in this class may consist of a pair of bones united by cartilage.

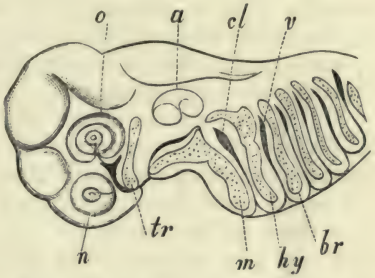

Fig. 820.—Left lateral view of the skull of an embryo Dog-fish. *tr*, Left trabecula; *n*, *o*, *a*, Nasal, orbital, and auditory capsules; *m*, *hy*, *br*, Mandibular, hyoid, and branchial arches; *cl*, *v*, Hyomandibular and first branchial clefts. (After Parker.)

The *skull*, or anterior termination of the axial skeleton, now claims our attention, but the description of this important and difficult part must be of the briefest. The researches of embryologists have shown that the skull is only a special modification of the primitive elements from which the rest of the axial skeleton were formed, although it does not consist, as was once thought, of a series of modified vertebræ. The skull is divisible into a dorsal, or *cranial*, and a ventral, or *visceral*, portion; the former, originating from a series of primitive segments (*somites*), encloses the brain-cavity; while the latter, which has a segmentation of distinct and later origin, is primitively connected with the function of respiration.

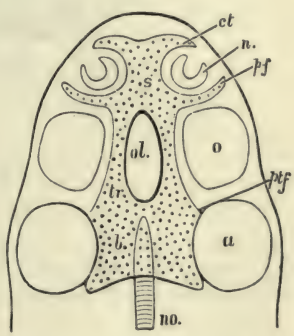

Fig. 821.—Upper view of a later embryo. *ct*, Cornu of trabeculæ; *pf* and *ptf*, Preorbital and postorbital processes of do.; *s*, Ethmonasal septum; *b*, Basilar plate; *no*, Notochord; *ol*, Olfactory foramen. Other letters as in fig. 820.

The earliest commencement of the primitive cartilaginous cranium occurs in the formation of a pair of rod-like *trabeculæ* (fig. 820), lying at the base of the brain, of which the posterior *parachordal* parts embrace the extremity of the notochord (fig. 821). These parachordals soon unite to form a *basilar plate* supporting the brain (fig. 821); while the anterior *prochordal* parts unite in front to enclose a space (*ibid.*, *ol*) for the passage of the olfactory nerves,

the united portion forming the *ethmonasal septum* (*ibid.*, *s*). By the approximation of the basilar plate to the *nasal*, *orbital*, and *auditory capsules*, these three distinct sense-regions become differentiated in the cranium; and while the first and third become enclosed in cartilage, the lateral borders of the basilar plate, in some instances, grow upwards to enclose the brain in a complete cartilaginous capsule, which in certain Sharks (fig. 822) persists throughout life. In the higher forms, however, the cartilage does not extend upwards over the brain, which becomes roofed in by bone formed directly from the overlying membrane.

The *visceral portion* of the skull is formed by cartilages arranged in a series of *arches* in the walls of the throat (fig. 820). In the Ichthyopsida there may be as many as nine of these *visceral arches*, but in the other three classes they become reduced in number to at most three or four, which are also functionally modified. The first arch (fig. 820, *m*) supports in all cases the walls of the mouth, and is accordingly called the *mandibular* arch; the second is termed the *hyoid;* while the remaining ones, which persist only in the adults of Fishes as supports of the gills or *branchiæ*, are termed *branchial*. It should further be observed that these arches are separated from

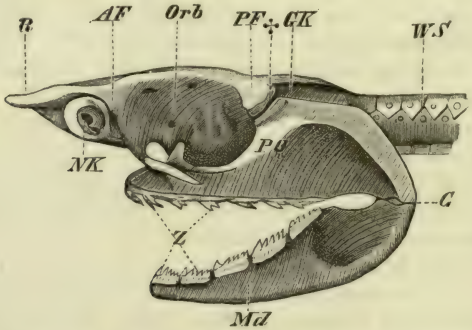

Fig. 822.—Left lateral view of the cartilaginous skull of a Shark (*Notidanus*), greatly reduced. *R*, Rostrum; *AF*, *PF*, Pre- and post-orbital processes; *Orb*, Orbit; *NK*, Nasal capsule; +, Articulation of palatopterygoid (*PQ*); *G*, Articulation of Meckel's cartilage (*Md*); *Z*, Teeth; *WS*, Vertebral column. (After Wiedersheim.)

one another in the embryo by a series of *visceral clefts* (fig. 820), of which the respiratory apertures of Sharks are remnants. The *mandibular arch* becomes divided into segments, consisting of a short proximal portion known as the *quadrate*, which very generally forms the main support of the lower jaw; and a long distal portion known as *Meckel's cartilage*, around which the *mandible*, or lower jaw, is subsequently formed in those forms which develop membrane bones, but which in the Sharks persists throughout life as the functional lower jaw

(fig. 820). The quadrate gives off an anterior *palatopterygoid* (*palatoquadrate*) bar, which in Sharks (fig. 822) persists to form a kind of false upper jaw. The hyoid arch, which is close to the mandibular, and which in Fishes may also take a share in the support of the mandible, is likewise segmented; the most important elements in the latter class being the *hyomandibular* and the *symplectic*, which are shown in an ossified condition in fig. 823, *hm*, *sy*. As already mentioned, in Sharks the primitive cartilaginous skull is complete, and persists in this condition throughout life; but in the great majority of Vertebrates the progress of chondrification is arrested,

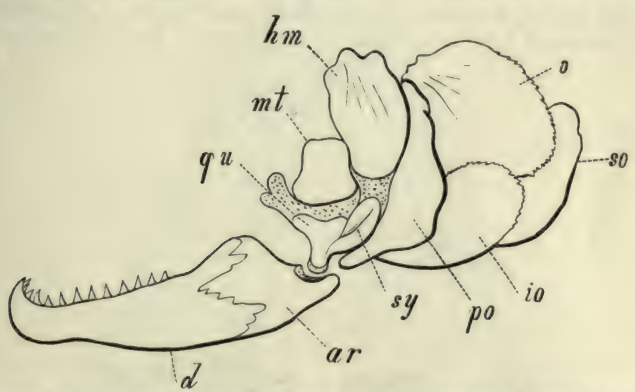

Fig. 823.—Left lateral view of the suspensorial and mandibular region of the skull of a Salmon. *hm*, Hyomandibular; *mt*, Metapterygoid; *qu*, Quadrate; *sy*, Symplectic; *po*, Preopercular; *io*, Interopercular; *so*, Subopercular; *o*, Opercular; *ar*, Articular; *d*, Dentary. (After Parker.)

and the skull becomes more or less completely covered in with a series of ossifications developed in the membrane overlying the brain, while the cartilaginous foundation itself is likewise converted into bone. Bones derived from these two totally distinct sources amalgamate in the adult in such a manner as to afford no clue to their dual origins. Following a modification of an arrangement adopted by Professor Weinsheimer, the more important bones of the cranium may be enumerated as follows: the relative position of most of them being shown in figs. 824 and 825.[1] The cartilage bones comprise the *basioccipital*, *basisphenoid*, and *presphenoid*, which are median ossifications (not shown in the two figures) lying in this order (from the posterior extremity) on the inferior aspect of the cranium, and the first forming the floor of the *foramen magnum*, or aperture by which the spinal cord enters the cranium, and the three being collectively known as the *basi-cranial axis*. On

[1] In the sequel the figures of the skulls of many reptiles, and more especially those of *Ichthyosaurus* and *Nothosaurus*, show the general relations of the bones of the skull to advantage.

the sides of the basioccipital we have the two *exoccipitals*, forming the lateral boundaries of the foramen magnum, and either alone or in conjunction with the basioccipital, the single or double *occipital condyles*, by which in the higher forms the cranium articulates with the atlas vertebra. The bony auditory capsule is composed typically of the *proötic*, *epiotic*, and *opisthotic*,[1] to which in Teleostean Fishes must be added the *sphenotic* and *pterotic;* but, as will be noticed below, some of these bones may unite, when they receive a distinct name. The *alisphenoids* and *orbitosphenoids* are paired bones developed in the trabecular region; while the single *ethmoid* and the paired *turbinals* occur in the nasal region. The position of the *quadrate* has been already mentioned. Among investing or

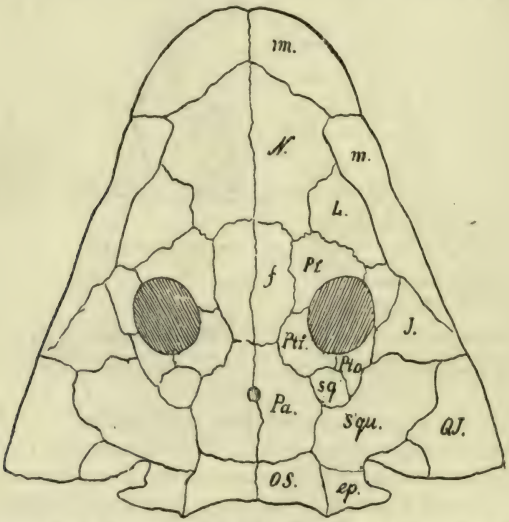

Fig. 824.—Upper surface of the cranium of a Labyrinthodont Amphibian (*Nyrania*), one-half natural size. *im*, Premaxilla; *m*, Maxilla; *N*, Nasal; *L*, Lachrymal; *f*, Frontal; *Pf*, Prefrontal; *J*, Jugal; *QJ*, Quadratojugal; *ep*, Opisthotic; *OS*, Supraoccipital; *Sq*, Squamosal; *Squ*, Supratemporal; *Pa*, Parietal; *Ptf*, Postfrontal; *Pto*, Postorbital. The quadrate would come below *QJ*; the large vacuities are the orbits; and the small aperture in *Pa* the parietal foramen. (After Fritsch.)

membrane bones, which are of a more or less splint-like structure, we have the following paired ossifications, reckoning from before backwards, on the upper surface—viz., *premaxilla* (*im*), *maxilla* (*m*), *nasal* (*N*), *lachrymal* (*L*), *frontal* (*f*), *prefrontal* (*Pf*), *postfrontal* (*Ptf*), *postorbital* (*Pto*), *parietal* (*Pa*), *supratemporal* (*Squ*), and *squamosal* (*Sq*). In some Dinosaurian Reptiles, as *Stegosaurus*, there appears to be a distinct bone above the orbit, which connects the pre- and postfrontal, and may be termed the supraorbital. The

[1] Shown in the skull of *Testudo*, figured in the sequel, fig. 1017A.

supraoccipital (*OS*), which, although double in the figured skull, is usually a single bone, appears to be developed inferiorly from cartilage and superiorly from membrane; it usually forms the upper border of the foramen magnum, and is not unfrequently produced posteriorly into a long spine. On the lateral aspect of the cranium are placed the *jugal* (*J*), and *quadratojugal* (*QJ*), which connect the quadrate with the maxilla; while inferiorly (fig. 825) we may have a median splint-like *parasphenoid* (*Ps*), and always a single or

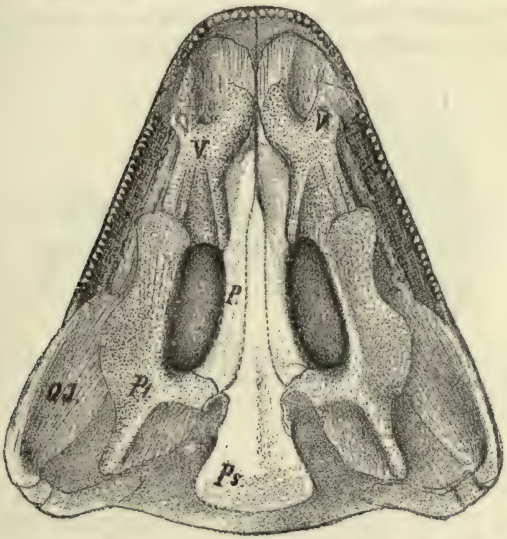

Fig. 825.—Under or palatal view of the cranium represented in fig. 824. *V*, Vomer; *P*, Palatine; *Pt*, Pterygoid; *QJ*, Quadratojugal; *Ps*, Parasphenoid. (After Fritsch.)

paired *vomer* (*V*), and the paired pterygoids (*Pt*), and palatines (*P*). The two latter, it may be observed, are developed upon the primitive palatopterygoid bar; while the parasphenoid, when present, underlies the basicranial axis, and if largely developed, as in Teleostean fishes and Amphibia (fig. 825), seems to take the place of the basi- and presphenoid.

In the cranium of which an upper view is given in fig. 824 the whole of the region behind the orbits is completely roofed over by bone, so that a secondary roof is thus formed above the roof of the much smaller brain-case which lies within. In most Reptiles there are, however, vacuities or fossæ in this outer roof (as in fig. 826), although in the Turtles and the Ichthyosaurs (fig. 1024) this roof persists. In fig. 826 the upper-lateral vacuity is termed the *supratemporal fossa*, and is bounded below by the *superior temporal* (or

squamoso-prefrontal) *arcade* formed by the squamosal, postorbital, and postfrontal; while the lower or *infratemporal fossa* is bounded superiorly by the last-named arcade, and below by an *inferior temporal* (or *quadrato-maxillary*) *arcade*, formed in most Reptiles (fig. 826) by the quadrate, quadratojugal, jugal, and maxilla. In the Mammalia (where it is usually termed the *zygomatic arch*) we find, however, a single arcade formed by the squamosal, jugal, and maxilla, and a similar arcade, but with the apparent absence of the jugal, occurs in many of the Anomodont Reptiles. This may be termed the *squamoso-maxillary arcade.* In many Sauropsida, when a postorbital or postfrontal is developed, these two arcades are

Fig. 826.—Right lateral aspect of the cranium of *Sphenodon punctatus*. The lower vacuity on the left is the infratemporal fossa, bounded below by the inferior, and above by the superior temporal arcade; the vacuity above the latter being the supratemporal fossa. The posterior border of the latter fossa is formed by the parieto-squamosal bar. The quadrate is on the left lower corner of the figure. (After Günther.)

usually connected behind the orbit by a process from the former articulating with another from the jugal, and thus forming a bar or arch which may be termed the *postorbital bar* or arch. Similarly another bar at the posterior extremity of the supratemporal fossa is formed by the quadratojugal (or quadrate), squamosal (the supratemporal of fig. 824 being absent), and parietal, and may be termed the *posttemporal*, or *parieto-squamosal bar*, or arch. A third fossa behind this bar is termed the *posttemporal fossa.* It will be observed that these numerous vacuities expose to view the brain-case lying within these arches or bars; and there seems to have been a gradual tendency to open up the completely roofed skull of the Labyrinthodont Amphibia till in the Mammals we find, as already mentioned, the squamoso-maxillary, or zygomatic arcade, and often a postorbital bar, as the sole remnants of this primitive secondary roof.

It will not be necessary to mention the various neural and vascular foramina of the cranium, but it must be observed that on the upper aspect there are paired apertures for the *orbits* (fig. 826), and either paired or single ones for the *nares* (*ibid.*); while between these apertures there may be the paired *preorbital vacuities*, which are shown

in the figure of the skull of *Phytosaurus* among the Crocodilia. Mention must also be made of the *parietal foramen* (fig. 824), which is a vacuity occurring in the parietals of many Reptiles and Amphibians. In several living forms this foramen immediately overlies an aborted median eye embedded in the subjacent tissues, and totally functionless; but it is not improbable that in the Labyrinthodonts and other early forms this eye served the purposes of vision. As the attention of the palæontologist is often directed to them, we must also observe that the *Eustachian tubes* are canals connecting the internal ear with the pharynx or gullet. Apart from certain minor ossifications which will be incidentally noticed in the sequel, we must also call attention to the *periotic* and *tympanic* of Mammals, since among the Cetacea these bones are of great importance to the palæontologist. Both these bones are connected with the internal ear, the first resulting from the coalescence of the proötic, epiotic, and opisthotic of the lower forms, and containing the *cochlea* of the ear; while the latter is formed by ossification in the tissues around the tympanic membrane, and also occurs in some Birds. Finally, the term *tympanic ring* is a convenient one to apply to the bones surrounding the external ear of Reptiles, and especially the Chelonia.

In regard to the *mandible*, or lower jaw, which we have already stated to be formed by ossifications in the region of Meckel's cartilage, each half, or *ramus* (fig. 827), in the Sauropsida and Am-

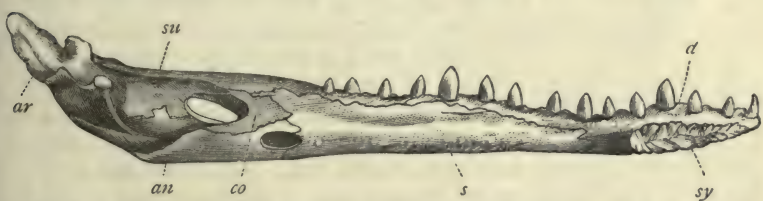

Fig. 827.—Inner view of the left ramus of the mandible of *Crocodilus*. *sy*, Symphysis; *d*, Dentary; *s*, Splenial; *co*, Coronoid; *an*, Angular; *su*, Surangular; *ar*, Articular. Reduced. (After Cuvier.)

phibia consists of the following five ossifications formed in membrane—viz., *dentary* (*d*), *splenial* (*s*), *coronoid* (*co*), *angular* (*an*), and *surangular* (*su*). These unite with the *articular* (*ar*), formed from Meckel's cartilage, which articulates by a *glenoid cavity* with the quadrate. In Mammals, however, there is but a single membranous ossification in each ramus, which posteriorly articulates by a rounded *condyle* with the squamosal bone of the cranium, there being apparently no articular ossification, and no distinct quadrate in connection with the mandible.[1] In the Sauropsida the quadrate articulates

[1] See the introductory chapter on the Mammalia (Chapter lvii.)

directly with the periotic region; but in the greater number of Fishes the mandible, as already mentioned, is connected with the cranium by means of the hyomandibular suspensorium (fig. 823).

Having now noticed the leading features of the axial, we may proceed to an equally brief survey of those of the appendicular skeleton. In all the higher Vertebrates the limbs are divided into three sections — viz., in the *pectoral* or fore *limb* the *arm*, *fore-arm*, and the *hand* or *manus;* and in the *pelvic* or hinder *limb* the *thigh*, *leg*, and the *foot* or *pes*. The first segment has a single bone—the *humerus* of the arm, and the *femur* of the thigh (fig. 828); the second has two parallel bones—the *radius* and *ulna* in the fore-arm, and the *tibia* and *fibula* in the leg (fig. 828); while the third segment contains a number of bones arranged in not more than five longitudinal rows (figs. 828, 829), with the exception of the Ichthyopterygian Reptiles. The bones of the manus and pes are again divisible into three sections—viz., proximally the *carpus* or wrist in the manus (fig. 829), and the *tarsus* or ancle in the pes; mesially the *metapodium*, or *metacarpus* of the manus (fig. 829), and the *metatarsus* of the pes (fig. 828); and distally the phalangeals (figs. 828, 829) of the digits. With the exception of the Ichthyopterygia, where the normal digits appear to have divided, in all known forms the number of functional digits does not exceed five; and these are enumerated consecutively from the radial or tibial side, so that the *pollex* or thumb of the manus, and the *hallux* or great toe of the pes are always termed the first, and the little finger and toe the fifth digits. Except in the hallux there are usually not less than three phalangeals in each digit of the pes, but their number may be reduced in the manus. The bones of the metapodium correspond in number with the digits, and consist of a single transverse row.

Fig. 828. — Dorsal aspect of right innominate and pelvic limb of the Chimpanzee (*Troglodytes*), reduced. *i*, Innominate; *f*, Femur; *t*, Tibia; *s*, Fibula; *r*, Tarsus; *m*, Metatarsus; *p*, Phalangeals. (After Owen.)

Although, as we have stated, the number of digits in the higher Vertebrates is typically five, yet there appears to be considerable evidence that the number was originally seven. Thus in many pentedactylate Mammals, and also in some Reptiles and Amphibians, there is found on the radial or preaxial border of the carpus or tarsus a small ossification which Dr Bardeleben terms the *prepollex*, or *prehallux*, and regards as

the representative of an additional radial digit. Similarly the *pisiform* bone of the carpus, which occurs on the ulnar or postaxial border, and in Mammals is usually described as one of the so-called sesamoid bones, is looked upon by the same authority as the representative of a seventh digit on the ulnar side.

It is probable that the carpus and tarsus were originally formed upon a common type, which persists in a more or less unaltered condition in certain Amphibia and Reptilia (fig. 829). In such a generalised type there is a distal row of five carpalia (fig. 829), or tarsalia, articulating with the metapodials. This is preceded proximally by another row, consisting of an *intermedium*, flanked in the manus by a *radiale* and *ulnare*, and in the pes by a *tibiale* and *fibulare*, respectively articulating with the two epipodial bones of the fore-arm (radius and ulna) or leg (tibia and fibula). The middle space between these two transverse rows of bones is occupied by one *centrale*, or occasionally by several *centralia*. Modifications from this type are caused by the suppression or coalescence of some of these elements. All the carpals and tarsals in the Mammalia have received distinct names, which will be noticed under the head of that class; but it may be observed here that the higher Reptiles and Birds agree with the former in having two bones in the proximal row of the tarsus —viz., the *calcaneum* on the fibular, and the *astragalus* on the tibial side.

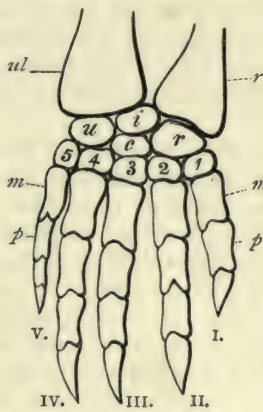

Fig. 829.—Dorsal aspect of the right manus of a Chelonian Reptile (*Chelydra*). *ra*, Radius; *ul*, Ulna; *r*, *i*, *u*, Radiale, ulnare, and intermedium; *c*, Centrale; 1—5, Carpalia; *m*, Metacarpals; *p*, Proximal phalangeals; I.—V., Terminal do., I. being the pollex. (After Gegenbaur.)

The protuberances for muscular attachment at the proximal extremity of the humerus are termed *tuberosities*, while those of the femur are known as *trochanters*. The latter bone in the Sauropsida may also have an *inner trochanter* on its shaft for the attachment of the *femoro-caudal* muscle; while in the Mammalia there may be a *third trochanter* for that of the gluteus maximus, as is shown in the femur of *Rhinoceros* represented in fig. 1226. Both the humerus and femur have more or less distinct *condyles* at the lower extremity for the articulation of the bones of the fore-arm and leg—those of the humerus being often termed *trochleæ*. Above the condyles or trochleæ the humerus has projecting *epicondyles* on either side; and there is frequently a foramen situated above either

the outer or inner epicondyle. When placed above the outer or radial epicondyle this foramen is termed *ectepicondylar*, and when above the inner or ulnar epicondyle *entepicondylar*. The proximal extremity of the ulna is often produced into an *olecranon* (fig. 1300), which projects behind the end of the humerus. The distal extremity of the tibia in certain Sauropsida develops from its anterior aspect a ridge or process known as the *cnemial crest;* while the *deltoid crest* or ridge is a prominence situated below the head of the humerus on the radial side, to which the attention of the palæontologist is not unfrequently directed. Finally, the *patella* is a so-called sesamoid bone developed in the tendon of a muscle passing over the pulley-like surface or trochlea on the anterior aspect of the distal extremity of the femur.

Since the limbs of Fishes differ considerably from the higher type of structure noticed above, their consideration may be deferred till we come to that class. Before, however, leaving the subject of limbs, it should be observed that it is often convenient to allude to the corresponding or homologous sides of the fore and hind limbs by a single term. If, then, we imagine the limbs extended more or less nearly at right angles to the axis of the body (as on the left side of fig. 814), with the palm of the hand and the sole of the foot directed to the front or ventral aspect, the middle digit of each limb will be *axial*, when the pollex and radius of the pectoral, and the homologous hallux and tibia of the pelvic limb, will be obviously *preaxial;* while the fifth digit of each limb, together with the ulna and the fibula, will be *postaxial*. The whole of the radial and tibial sides of the limbs will accordingly be known as the *preaxial*, and the ulnar and fibular as the *postaxial border*.

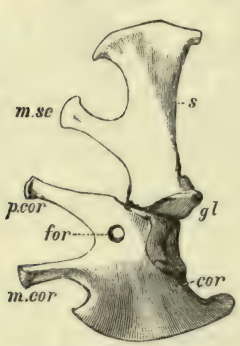

Fig. 830.—Lateral aspect of the cartilage bones of the left side of the pectoral girdle of a Lizard (*Iguana*). *s*, Scapula; *m.sc*, Mesoscapular process of do.; *cor*, Coracoid; *p.cor*, Precoracoidal process of do.; *m.cor*, Mesocoracoidal process of do.; *for*, Foramen of do.; *gl*, Glenoid cavity.

The remaining parts of the skeleton comprise the *pectoral* and *pelvic girdles*, by which the corresponding limbs are respectively connected with the trunk, and of which the relative positions are shown in fig. 818. The pectoral arch is never connected by means of ribs with the vertebræ, and primitively consists of three main bones developed in cartilage. On the dorsal aspect of the body we have the upper bone or *scapula* (fig. 830, *s*); while on the ventral side there are two parallel bones (fig. 974), the anterior of which is termed

the *precoracoid* (*cl*), and the posterior the *coracoid* (*co*). At the junction of these three bones there is a cavity for the articulation of the head of the humerus termed the *glenoid cavity*. Such is the primitive condition of this girdle; but in Reptiles the precoracoid very rarely exists as a separate ossification, although it does so among the Anomodonts, where, at least in the young, it forms a large plate, uniting below to the upper edge of the coracoid, and entering into the formation of the glenoid cavity.[1] In all other cases it is, however, completely fused either with the scapula or the coracoid. Thus in the Chelonia (fig. 1008) the precoracoid retains its primitive form and condition of a transverse bar, which is, however, completely fused with the scapula. In the Lizards, on the other hand, this bone has united with the coracoid, of which it forms the precoracoidal process (fig. 830, *p.cor*)—the foramen (*for*) marking the original line of separation between the two bones. In Dinosaurs and many other Reptiles the precoracoidal process has disappeared, and only the foramen remains; while in the Ichthyopterygia even this is wanting. A further reduction occurs in the higher Mammals, where the whole of the coracoid has disappeared as a distinct bone. The coracoid is subject to great variation in shape, and may either simply meet its fellow by an overlapping or sutural junction, or may articulate with the sternum.

A *clavicle*, mainly developed from membrane, may be connected with the preaxial borders of the scapula and coracoid; while a mesial T-shaped *interclavicle* (fig. 819), which is also developed from membrane, may receive the inner extremities of the two clavicles, and then usually overlies the upper part of the sternum. Finally, there may also be a single or double mesial *omosternum* developed on the ventral aspect from cartilage lying near the anterior extremity of the girdle. An illustration of the position of this bone is shown in the pectoral girdle of the Frog, represented in fig. 974.

In the pelvic girdle we have three separate ossifications arising in cartilage, of which all three usually unite to form an *acetabulum* (fig. 831,[2] *a*, *b*) for the reception of the head of the femur, or thigh-bone. The bone commonly known as the haunch-bone forms the dorsal element, and is technically termed the *ilium* (*ibid.*, *Il*); it corresponds to the scapula, and usually articulates with the sacrum by short ribs; while in the ventral half we have anteriorly the *pubis* (*ibid.*, *P*), representing the precoracoid; and posteriorly the *ischium* (*ibid.*, *Is*), which corresponds to the coracoid. The two latter bones

[1] This precoracoid appears to correspond with the bone termed *epicoracoid* by Professor Cope, and also the one so named in the Monotreme Mammals.

[2] Here the acetabulum is formed by only two bones, and it has been suggested that the bone lettered pubis may be really an epipubis.

very generally meet those of the opposite side in a ventral symphysis; and when, as is frequently the case, the three bones of either side are anchylosed together, an *innominate* bone results (fig. 1128 *bis*). The ischium and pubis of the same side may also unite inferiorly so as to enclose the *obturator notch*, *F*, which then forms the *obturator foramen* (fig. 1128 *bis*); while an *obturator process* of the ischium may form a smaller foramen below the acetabulum, as in the pelvis of *Camptosaurus*, figured in the sequel (fig. 1052). As a rule, there is no tendency to a reduction in the number of the pelvic bones in the higher forms. It may be mentioned, in conclusion, that a median ossification at the ventral symphysis of the pubis and ischium found in certain *Edentates* has been named the *pelvisternum*, and regarded as the abdominal representative of the sternum. This appears, however, to correspond with the median ossification found in the Ungulates (fig. 1128 *bis*), which is generally looked upon merely as an epiphysis. The pectoral and pelvic girdles of Fishes are noticed in the next chapter.

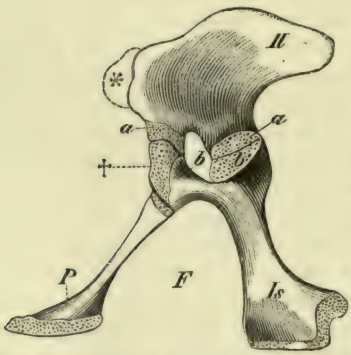

Fig. 831.—Lateral aspect of the left half of the pelvis of a young Crocodilian (*Alligator*). *Il*, Ilium; *P*, Pubis; *Is*, Ischium; *F*, Obturator notch; *a*, *b*, *b*, Acetabulum, with its vacuity; †, *, Cartilaginous extensions of ilium.

It may be well to observe here that genera being purely and simply artificial divisions formed for the convenience of classification, it is quite unnecessary that they should be of equivalent value in different groups of animals. As examples of vertebrate groups in which generic terms are used in a wide sense, we may cite the Reptilan order Sauropterygia and the Mammalian family *Rhinocerotidæ*; while as instances where a more restricted application is employed, we may mention the order Chelonia, and the family *Bovidæ*. The statement we not unfrequently hear that such-and-such a form *must* represent a distinct genus implies a total misconception of the import of generic terms.

CHAPTER XLVI.

CLASS PISCES.

General Structure.

The members of the class Pisces, commonly known as Fishes, form the first division of Professor Huxley's Ichthyopsida, and are generally characterised by living in water; breathing by branchiæ, or gills, throughout life; having the heart furnished with a single ventricle and auricle (atrium); having the limbs, when present, in the form of fins; being provided with unpaired median fins supported by fin-rays; and by the skin being either naked, or covered with dermal scales or bony scutes. There is no amnion or allantois developed in the embryo, and the reproduction is nearly always oviparous. Certain forms do not, however, exhibit all the above features, and the relation of the more generalised Fishes to the Amphibia is very intimate. The peculiar system of mucous canals and the lateral line are highly characteristic of Fishes, although they are not invariably present.

Before noticing such features as are of especial importance to the palæontologist, it will be convenient to mention that according to the arrangement adopted in this work the class is divided into the following six orders—viz., Cyclostomi, Elasmobranchei, Chimeroidei, Dipnoi, Ganoidei, and Teleostei, of which the salient features will be noticed in the succeeding chapter. Dr Günther has, indeed, proposed to bracket together the second, third, fourth, and fifth orders as a subclass under the name of Palæichthyes, ranking as equivalent to the Cyclostomi and Teleostei. Professor Huxley, Dr Traquair, and others have, however, shown that the Ganoidei are so intimately connected with the Teleostei, while the Elasmobranchei, Chimeroidei, and Dipnoi differ in so many respects among themselves and from the former, that such a grouping does not appear consonant with their true relationship.

Another scheme, proposed by Professor Cope and adopted by

Mr Smith-Woodward, is to brigade the Teleostei and Ganoidei together in a subclass under the name of Teleotomi, with ordinal divisions differing somewhat from the subordinal ones employed below, and to raise the Dipnoi, Chimeroidei, Elasmobranchei, and Cyclostomi to the rank of subclasses, with the concomitant elevation of their respective suborders to the rank of orders. It seems, however, scarcely to harmonise with the divisions adopted in the other classes of Vertebrates to regard a group like the Chimeroidei as a subclass, and accordingly the view of Professor Huxley is provisionally followed of regarding the Elasmobranchei and Chimeroidei as divisions of ordinal value.

Although the body in all Fishes must be adapted for progression through the water, yet there is an enormous range of variation in its contour among the different groups, as we may observe when we contrast a Lamprey, a Shark, a Flat-fish, a Ribbon-fish, and a Globe-fish. The dermal structures termed scales, which are so characteristic of Fishes, present many types of structure. In the Teleostei they usually form thin plates, frequently marked by concentric lines and not formed of true bone.

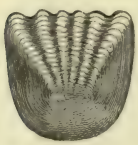

Fig. 832.—Cycloid scale, enlarged.

Fig. 833.—Ctenoid scale, enlarged.

When the posterior margin is simple (or entire) such a scale is termed *cycloid* (fig. 832), but when denticulated, *ctenoid* (fig. 833). Other examples of this type are shown in figs. 834, *a*, *b*. In many Ganoids and a few Teleosteans the scales are much thicker, and consist of a variety of true bone covered externally with an enamel-like substance termed *ganoine*. Such scales, of which specimens are shown in fig. 834, *e*, and fig. 835, are termed *ganoid*; they are arranged in oblique rows, and connected together by a peg-like projection, their shape being oblong. Scales of ganoid structure may, however, be much thinner, and resemble the cycloid type in their contour and their imbrication. Lastly, the bony dermal scutes or plates, frequently armed with a spine, which occur in the skin of the Sharks and Rays (fig. 834, *c*, *d*), are strictly comparable in structure to teeth, consisting of

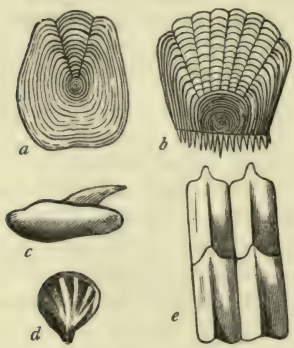

Fig. 834.—*a*, Cycloid scale of Pike (*Esox*); *b*, Ctenoid scale of Perch (*Perca*); *c*, Dermal plate of Thornback (*Raia*); *d*, Do. of Monkfish (*Squatina*); *e*, Ganoid scales of *Palæoniscus*. *a* and *b* enlarged.

a cap of enamel underlain by dentine and supported on bone. Allied to these are the calcified scutes of the Coffer-fishes (*Ostracion*), File-fishes (*Balistes*), and Sturgeons (*Acipenser*), to all of which structures the term *placoid scales* was formerly applied. A characteristic feature in the Teleostei is the presence of a series of perforated scales running along the side of the body, known as the *lateral line*, the canal of this line being apparently in part connected with the supply of mucus, and acting partly as a sense-organ. The modified scales of this line may be larger or smaller than those of the rest of the body, or may be the only ones present. A lateral line is also found in some Ganoids and in certain Elasmobranchs, as well as in the Chimeroids. A series of large V-shaped scales found on the borders of the fins of many Ganoids are termed *fulcra*. The dermal fin-rays are peculiar to the present class, and are shown in figs. 836, 837. They

Fig. 835.—Ganoid scale.

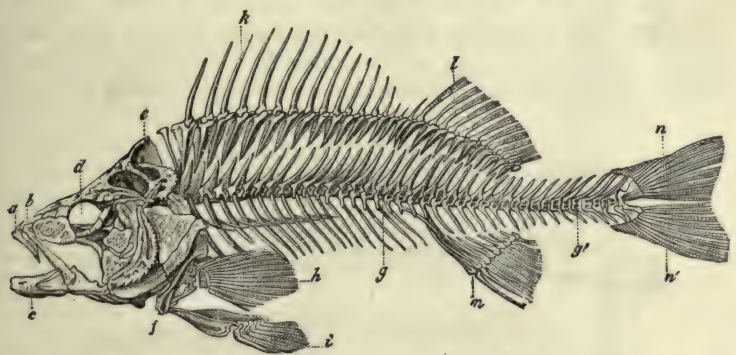

Fig. 836.—Reduced left lateral view of the skeleton of the Perch (*Perca*). *a*, Premaxilla; *b*, Maxilla; *c*, Mandible; *d*, Orbit; *e*, Supraoccipital; *f*, Preoperculum; *g*, *g'*, Vertebræ; *h*, Pectoral fin; *i*, Pelvic do.; *k*, *l*, First and second dorsal do.; *m*, Anal do.; *n*, *n'*, Caudal do. The bones between *k* and *l* and the vertebræ are the interspinals.

occur both in the paired *pectoral* and *pelvic* fins, and also in the median *dorsal*, *caudal*, and *anal* fins. In Elasmobranchs these fin-rays are horny; but in the Teleostei (fig. 836) they are bony, and generally split up into filaments at the extremities (*l*), although they may be pointed (*k*). In Teleostei they generally consist of two closely applied parts, diverging at the base to articulate in the median fins with the interspinous bones of the endoskeleton, and in the paired fins with the distal limb bones. In Elasmobranchs the interspinals are represented by the so-called radial cartilages belonging to the true endoskeleton.

In Teleosteans and Ganoids the anterior rays of the dorsal and

pectoral fins may be developed into huge dermal spines, which in some cases articulate by a complete shackle-joint with the basal bones. Similar spines are also developed in the Elasmobranchei

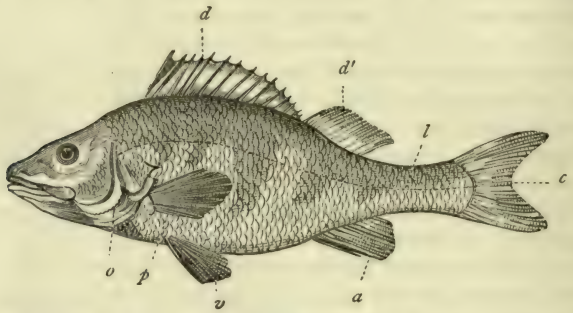

Fig. 837.—Left lateral view of the Perch (*Perca*). *o*, Gill-cover, with gill-slit behind it; *p*, Pectoral fin; *v*, Pelvic do.; *d*, First dorsal do.; *d'*, Second dorsal do.; *l*, Lateral line. Reduced.

(fig. 838); but here they are simply inserted into the flesh, or are attached only by cartilage, so that their basal end is rounded off. Similar spines (fig. 838, 1) may also occur behind the head. Such

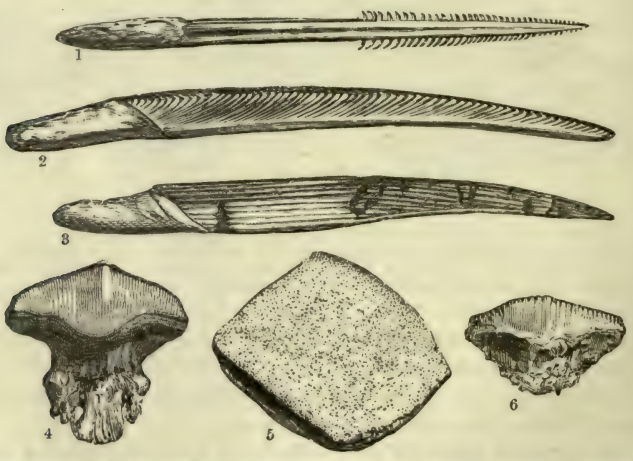

Fig. 838.—Spikes and teeth of Elasmobranchei. 1, Nuchal spine of *Pleuracanthus*; 2, Fin-spine of *Gyracanthus*; 3, Do. of *Ctenacanthus*; 4, Tooth of *Petalodus*; 5, Do. of *Psammodus*; 6, Do. of *Ctenoptychius*. Carboniferous. 1–3 are reduced.

spines when found fossil are frequently known as *ichthyodorulites*, and form important objects to the palæontologist. Their structure is identical with that of the so-called placoid scales and of teeth,

there being a central pulp-cavity, surrounded by a layer of dentine or vasodentine, which is covered with enamel.

The teeth of Fishes present a greater amount of variation than is found in any other class. They may be entirely absent, or may be present on all the bones of the mouth, and also on the hyoids and branchial arches, while they may be attached merely to the membrane of the mouth-cavity. Very frequently they are attached by anchylosis to the underlying bone or cartilage (fig. 838), but they may be implanted in distinct sockets or alveoli. The dentine is usually distinguished from that of the teeth of higher Vertebrates by its greater vascularity. The coating of enamel is generally very thin; but it is more developed in the cutting-teeth of *Sargus*. Occasionally (*Dendrodus*) radiating prolongations of the pulp-cavity may penetrate the dentine from the centre to the periphery, thus producing a structure like that of the teeth of the Labyrinthodont Amphibians. There is generally a constant renewal of the teeth of Fishes during the whole of life; but occasionally one set persists.

Fig. 839.—Anterior aspect of a caudal vertebra of a Teleostean Fish *ns*, Neural spine; *na*, Neural arch; *z*, Articular processes; *ha*, Hæmal arch; *hs*, Hæmal spine. (After Günther.)

Turning to the endoskeleton, and commencing with the vertebral column, we find that the vertebræ can only be divided into a trunk and a caudal series, and that there is a gradual progression in respect of ossification from the lowest to the highest forms. Thus, in the Cyclostomi, the notochord persists throughout life, and is generally unsegmented, although rudimental neural arches and spines are developed in *Petromyzon*. The vertebral column of the Cartilaginous Ganoids is very similar to that of the latter; but in Bony Ganoids, Elasmobranchei, and Teleostei paired cartilages, arising both above and below the notochord, gradually surround it, and thus form strongly amphicœlous vertebral centra. In the Sharks these centra exist without arches, but in the other orders there are well-developed neural arches; and in the trunk region there are also lateral *basal processes*, which in the tail unite inferiorly to form a hæmal arch for the caudal artery, and develop a hæmal spine (fig. 839). There is a great tendency for the neural arches to remain open superiorly; and the only Fish in which the vertebræ are not amphicœlous is the Ganoid *Lepidosteus*, in which they are opisthocœlous. Only in the Chimeroidei and certain Elasmobranchei are there definite articulations between the vertebral

column and the cranium; the posterior aspect of the basioccipital in other groups forming a cup like that of a vertebral centrum. The mode in which the vertebral column terminates posteriorly is of considerable importance in classification. The most primitive

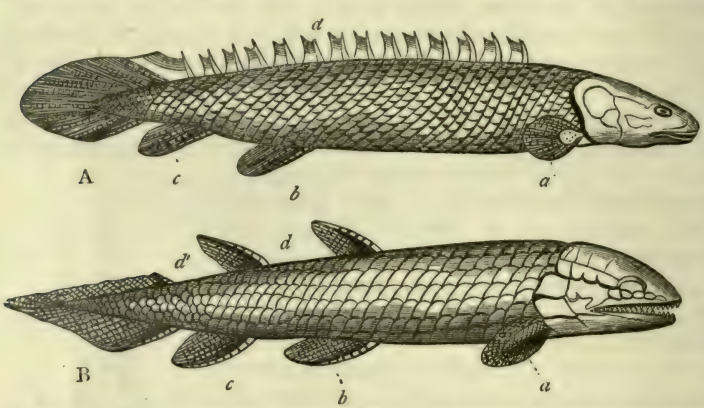

Fig. 840.—A, *Polypterus*, and B, *Osteolepis* (Ganoids), to show diphycercal caudal fin. *a*, Pectoral; *b*, Ventral; *c*, anal; *d*, Dorsal fin. Reduced.

type occurs in the Cyclostomi, Dipnoi, and many Ganoids, where the notochord continues to the extremity of the body, and is symmetrically surrounded by the caudal fin, as in fig. 840; this type is known as *diphycercal*. In the other, or *heterocercal* type, the notochord

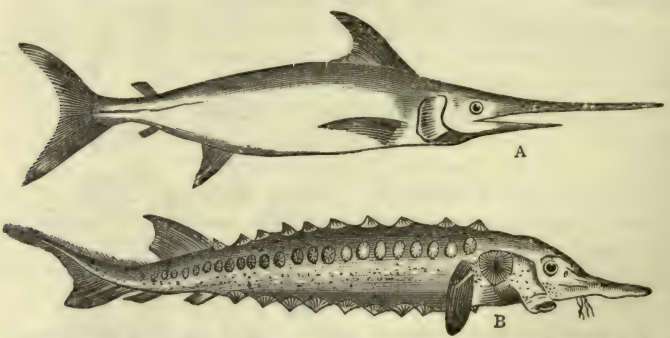

Fig. 841.—A, Sword-fish; B, Sturgeon, to show masked (homocercal) and typical heterocercal tail.

is bent upwards, owing to the greater development of the lower as compared to the upper half of the tail. This feature may be observable externally, as in the Sturgeons (fig. 841, B) and Sharks; or may be masked, as in the majority of Teleostean Fishes (fig. 841, A), by the symmetrical arrangement of the fin-rays. The skeleton (fig.

842) shows, however, the upward bend of the notochord, although this is very much less marked in the adult than in the young. This masked heterocercal type is sometimes described as *homocercal*. The coalesced hæmal spines found in this type of tail are known as *hypural* bones (fig. 842, *h*), while the ossified extremity of the notochord is termed the *urostyle*.

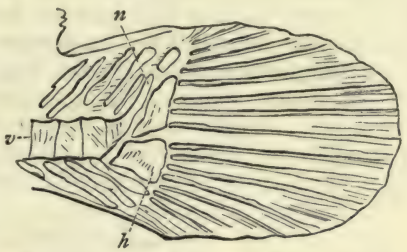

Fig. 842.—Tail of Flounder. (After Agassiz.) *v*, Vertebral column; *n*, Turned-up end of the notochord; *h*, Hypural bones.

The skulls of Fishes present variations in regard to their degree of ossification, analogous to those obtaining in the vertebral column. The general structure of the primitive cartilaginous skull has been already indicated in Chapter xlv. (fig. 822), but we must here glance briefly at certain bones developed in the more specialised forms which are peculiar to the class. Thus, taking as an example the skull of a Teleostean Fish (fig. 843), where the primitive cranium is concealed by the development of investing bones, we find two peculiar ossifications in the auditory region known as the pterotic (*ibid.*, *Pte*), which is considered to represent the squamosal and opisthotic of higher Vertebrates, and the sphenotic (*ibid.*, *Sph*). A large parasphenoid is always present inferiorly (fig. 844). The intervention of the hyomandibular and symplectic (figs. 823 and 843) between the quadrate and the squamosal region has been already mentioned in Chapter xlv. as peculiar to Fishes (although it is by no means universal in the class); and we must also mention that, in addition to the normal palatine and pterygoid bones developed

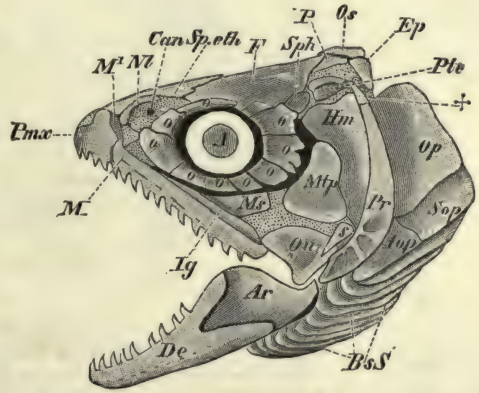

Fig. 843.—Left lateral view of the skull of a Trout (*Salmo*). *Ep*, Epiotic; *Pte*, Pterotic; *Sph*, Sphenotic; *Os*, Supra-occipital; *P*, Parietal; *F*, Frontal; *Sp.eth*, Ethmoid; *Can*, Aperture of olfactory nerve; *Nl*, Nasal; *Pmx*, Premaxilla; *M*, *M*¹, Maxilla; *Ig*, Jugal; *Ms*, Mesopterygoid; *Mtp*, Metapterygoid; *o*, *o*, Suborbitals; *Hm*, Hyomandibular; *s*, Symplectic; *Qu*, Quadrate; *Pr*, *Iop*, *Sop*, Pre-, inter-, and subopercula; *Op*, Operculum; *BsS*, Branchiostegal rays; *Ar*, Articular; *De*, Dentary; *A*, eye. (After Wiedersheim.)

round the cartilaginous palatopterygoid bar, there occur in Teleostei the *meso-* and *metapterygoid* (fig. 843, *Ms*, *Mtp*). In the same class the orbital region likewise develops a series of membrane-bones round the eye, forming the *suborbitals* or *orbital ring* (*ibid.*, *o*, *o*), while the *gill-cover* or *operculum* (of which the first trace is found in the Chimæroids in a fold from the hyomandibular overlapping the first gill-slit) is formed by the *preopercular*, *opercular*, *subopercular*, and *infraopercular* (*ibid.*, *Pr*, *Op*, *Sop*, *Iop*), which are broad, scale-like membrane bones. In the *branchiostegal membrane*, which unites with the gill-cover in closing the branchial chamber, there is developed a number of *branchiostegal rays* (fig. 843, *BsS*, and fig. 844, *bo*); but these may be partly or entirely replaced by

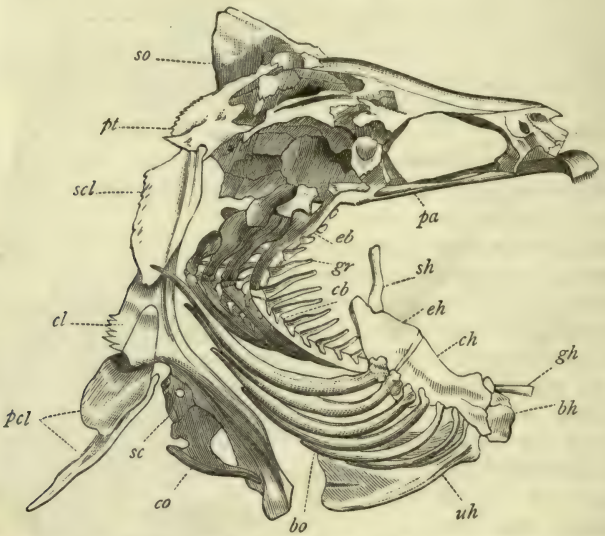

Fig. 844.—Right side of the cranium proper of a Perch, together with the hyoid and branchial arches, and the pelvic girdle. *sh*, Stylohyal; *eh*, Epihyal; *ch*, Ceratohyal; *bh*, Basihyal; *gh*, Glossohyal; *uh*, Urohyal; *bo*, Branchiostegal rays; *cb*, Ceratobranchial; *eb*, Epibranchial; *gr*, One of the "gill-rakers" of the first branchial arch; *pa*, Parasphenoid; *so*, Supraoccipital; *pt*, Posttemporal; *scl*, Supraclavicular; *cl*, Clavicular; *pcl*, The two pieces of the postclavicular; *sc*, Scapula; *co*, Coracoid.

jugular plates, occupying the space between the rami of the mandible. The hyoid arch (fig. 844) is attached to the inner side of the hyomandibular by a *stylohyal* (*ibid.*, *sh*), articulating inferiorly with the *epihyal* (*eh*), and the latter with the large *ceratohyal* (*ch*); the two latter carrying the branchiostegals. The inferior part of this arch is formed by the *basihyal* (*bh*), from which the *glossohyal* (*gh*) extends forwards into the tongue, and posteriorly articulates with the first of the *basibranchials*, mentioned below. The *urohyal*

(*uh*) is a vertically-compressed median bone, extending backwards from the basihyals. Behind the hyoid arch occur the *branchial arches*, the first of which consists of a median *basibranchial*, and laterally from below upwards of a *hypobranchial*, *ceratobranchial* (fig. 844, *cb*), *epibranchial* (*eb*), and *pharyngobranchial*. The latter bones in the second and third arches are called *superior pharyngeals*, and generally carry teeth. Finally, the *gill-rakers* (fig. 844, *gr*) are spine-like bones attached to the inner margins of the branchial arches.

In the mandible there is usually (fig. 843) a dentary and articular piece; but an angular, and more rarely a splenial or coronoid, may also be present.

In the appendicular skeleton, we find the pectoral girdle of Ganoids and Teleosteans consisting inferiorly of the primary cartilaginous elements corresponding to the scapula and coracoid (fig. 844, *sc*, *co*), and superiorly and laterally of a secondary chain of bones developed from membrane, and articulating superiorly with the pterotic region of the skull. The bones of this secondary chain are named from above downwards *posttemporal* (fig. 844, *pt*), *supraclavicular* (*scl*), *clavicular* (*cl*), and a *postclavicular* of two pieces (*pcl*); while there may be also an *infraclavicular* below the clavicular. In Elasmobranchei only the cartilaginous primitive girdle is developed; while in Dipnoi the girdle is of very peculiar structure, and somewhat intermediate between that of Elasmobranchei and Teleostei. The pelvic girdle is generally wanting; but in the Dipnoi there is a median cartilaginous plate, with anterior and posterior paired processes, of which the former are iliac, and the latter give attachment to the hind limbs. Elasmobranchs generally show a degenerate pelvis of this type.

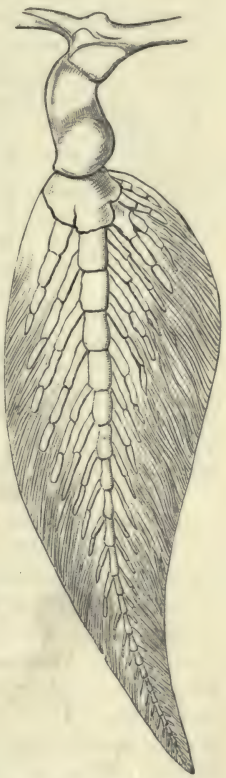

Fig. 845.—Skeleton of the left pectoral limb of *Ceratodus*. Reduced. (After Günther.)

The pectoral and pelvic limbs, or fins, are so similar in structure that they may be considered together, although the development of the latter is less specialised than that of the former. No representatives of the arm and fore-arm of the higher Vertebrates can be detected in Fishes, the basal and radial bones or cartilages articulating directly with the pectoral

girdle. In the Dipnoi, and especially in *Ceratodus*, the pectoral (fig. 845) and pelvic fins are supported by a cartilaginous, median, segmented axis, bearing jointed radii on the dorsal and ventral borders—these radial cartilages being terminated by horny dermal fin-rays; and the dorsal radii (left side of figure) being more numerous than the ventral. This type of fin, which also occurs in the Ichthyotomous Elasmobranchei, is known as the *archipterygium*. From this slightly unsymmetrical type of fin that of existing Selachian Elasmobranchs (fig. 846) may be derived by the gradual suppression of the ventral series of rays, and the development of the dorsal, which has now become lateral. Basally the jointed radial cartilages articulate proximally with the *pro-*, *meso-*, and *metapterygium*, which in their turn are attached to the pectoral arch, and the latter of which corresponds to the basal axial cartilage of the fin of *Ceratodus* (fig. 845). In the pelvic fin of the Selachians the mesopterygium is absent, and the propterygium more or less rudimentary. This type of fin is known as the *ichthyopterygium*. The fins of Ganoids and Teleosteans may be derived from the Selachian type; but the primary cartilaginous skeleton is reduced, and a secondary one developed by the introduction of membrane bones.

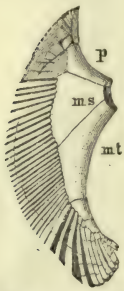

Fig. 846.—Skeleton of the left pectoral limb of the Monkfish (*Squatina*). *p*, Pro-; *ms*, Meso-; *mt*, Metapterygium. Much reduced.

Before leaving the structure of Fishes, mention must be made of the *otoliths*, which are small, rounded, elliptical bodies, usually with one convex and one concave side, lying in the tympanic sac, and composed of both calcic carbonate and phosphate. These bodies have been carefully studied by Dr Koken, and several genera identified by their evidence in a fossil state.

As regards their distribution in time, Fishes being the lowest class of the Vertebrata, it would naturally be supposed that they were the earliest representatives; and this appears to have been the case. The earliest known fishes in Britain belong to the Ganoid group *Placodermata*, and occur in the Lower Ludlow group of the Silurian; while the Elasmobranchei were represented in the topmost group of the same series. In the Devonian and Carboniferous periods Fishes become abundant; but all the forms from these horizons, and up to the Cretaceous, belong to the Elasmobranchei, Chimæroidei, Dipnoi, and Ganoidei—the specialised Teleostei not making their appearance, so far as we know with certainty at present, till the Cretaceous. The Ganoids of the suborder Amioidea approximate, however, so closely to the Teleostei, that it has been a question whether some of the members of the Jurassic family *Lepto-*

lepididæ, which are usually placed in the former, should not be transferred to the latter group; and we may thus confidently expect to find a complete transition between the two. Although many of the Cretaceous Teleostei are more or less closely allied to existing types, it is not until the Eocene that we find a fish-fauna comparable to that of the present day; and we may note that the resemblance of the fishes of the Eocene to those now living is in marked contrast to what obtains in Mammals, where the majority of Eocene genera are extinct. The persistence of some genera of Fishes throughout long geological epochs is indeed a noteworthy circumstance, and is nowhere more marked than in the case of *Ceratodus*, which has lived on continuously from the Triassic period of Europe, and also from that of certain North American beds, which are usually referred to the Permian.

In regard to the origin of the various orders of Fishes, it is pretty evident that the Teleostei were derived from the Ganoidei, and that the Dipnoi were closely related to one branch of the latter. The

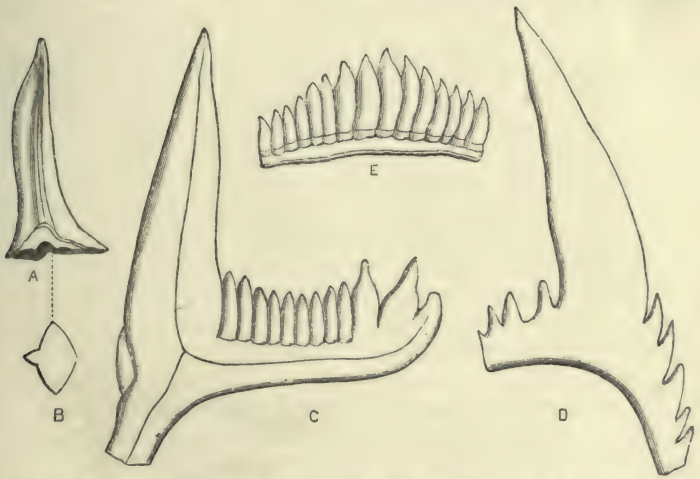

Fig. 847.—Conodonts, greatly enlarged. A, B, *Acodus acutus*; C, D, *Prionodus elegans*; E, An unnamed form; A–D, From the Silurian of Russia; E, From the Carboniferous of North America. (After Pander and Newberry.)

phylogenetic relationship of the Ganoids to the Elasmobrancheans is, however, still unsettled, although recent researches tend to show a close connection between the more primitive and least specialised groups of the two orders. Palæontology has not, indeed, yet taught us from what group of animals these primitive Ganoids and Elasmobranchs were themselves derived. It has, however, been suggested by Professor Cope that the Placodermoid Ganoids were closely re-

lated to the Ascidian Invertebrates; and if this suggestion should prove well founded, it would seem to indicate that the group mentioned is closely allied to the real ancestors of the class. Possibly, however, these ancestors are to be sought in another direction, since it has been thought that minute tooth-like bodies found in beds ranging from the Upper Cambrian to the Carboniferous, and known as *Conodonts* (fig. 847), are really the teeth of Fishes. It was considered probable at one time that these curious fossils, which rarely exceed two millimetres in length, might be teeth of extinct members of the Cyclostomi; but their internal structure is so different from the teeth of the existing forms of that order, that if they belong to Fishes at all, they must apparently indicate an extinct division. A great variety of forms of these Conodonts have been described, and have received distinct generic and specific names. It is the opinion of some authorities whose judgment is entitled to great consideration that these fossils should be regarded as the jaws of Annelids[1] or Trilobites; but the question as to their real nature must be regarded as still undecided.

[1] *Vide supra*, vol. i. p. 480.

CHAPTER XLVII.

CLASS PISCES—*continued.*

Orders Cyclostomi and Elasmobranchei.

Order I. Cyclostomi. — The Cyclostomi, which include the Hag-fishes (*Myxine* and *Bdellostoma*) and Lampreys (*Petromyzon*) being at present unknown in a fossil state, require no further notice in the present work.

Order II. Elasmobranchei.—This order, which is also known under the name of Chondropterygii, includes a peculiar extinct group termed the Ichthyotomi, together with the modern Sharks, Dog-fishes, Saw-fishes, and Rays, collectively constituting the Selachii, and all of which are typically of marine habits. For palæontological purposes this order may be characterised as follows: The skeleton is invariably cartilaginous, and membrane bones are, with some possible exceptions, absent in the skull; the vertebral column is, however, generally divided into distinct segments, of which the centra may be marked by a calcification differing in structure from true bone. In the skull, which may be either movably or immovably connected with the vertebral column, the palatopterygoid bar and hyomandibular suspensorium are never fused with the cranium. When an exoskeleton is developed, it consists of small dermal granules, of which the structure is the same as that of teeth. In all existing forms the optic nerves simply cross one another, without any interlacing of their component fibres; the bulbus arteriosus of the heart has three series of valves; the intestine is furnished with a spiral valve; and the ova are of large size and few in number.

A few words may be said explanatory of some of the above-mentioned and other features in existing forms before proceeding to the systematic part. In all forms, as already mentioned, there is a separate suspensorial arrangement articulating with the cranium, to which the mandible is attached; this structure being termed *hyostylic*. Usually there is a hyomandibular suspensorium intervening

between the cranium and the palatopterygoid bar; but in *Notidanus* (fig. 861) the hyomandibular element takes no share in the support of the mandible, and the palatopterygoid articulates directly with the cranium; this probably being the primitive type. The gills (fig. 848) are attached to the skin by their margins; while they usually communicate with the exterior by five apertures, or clefts, which may be very rarely increased to six or seven. The mouth is very generally situated on the inferior aspect of the body (fig. 849), and is furnished with numerous teeth carried on the palatopterygoid bar and Meckel's cartilage (fig. 861). These teeth may be either sharp and separate, or articulated together so as to form a more or less pavement-like structure; and in the former case there is a continuous succession of new teeth developed from behind as the old ones are worn out. Both median and paired fins are present; the position of the pelvic pair being always abdominal. In all existing forms the skeleton of the limbs forms an *ichthyopterygium* (fig. 846); but in the Carboniferous and Permian Ichthyotomi there is either a uniserial or biserial *archipterygium*, like that of the Dipnoi. The posterior termination of the vertebral column is generally heterocercal, with the upper lobe of the caudal fin greatly elongated (fig. 849). The spines frequently borne by the dorsal fins and in the nuchal region, constituting the so-called ichthyodorulites, have their bases simply embedded in the flesh, and are consequently immovable. There is no swim-bladder. The term *spiracles* is ap-

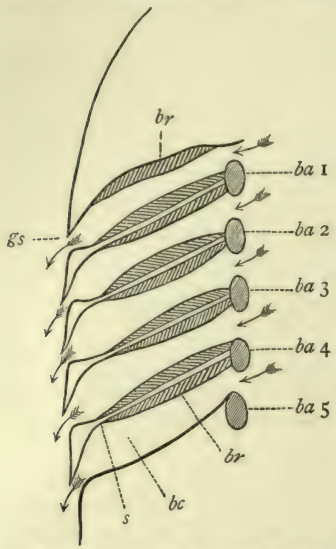

Fig. 848.—Diagram of one side of the gills and gill-pouches in a Selachian; the arrows indicating the direction of the currents. *ba* 1–5, Branchial arches transversely divided; *bc*, Branchial pouches; *gs*, External gill-slits; *s*, Septa between pouches; *br*, Branchiæ.

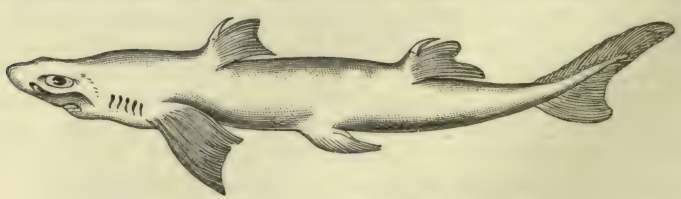

Fig. 849.—Spiny Dog-fish (*Acanthias*). Reduced.

plied to apertures connected with respiration found on the upper aspect of the head; while the *intercalary cartilages* are ovoid or diamond-shaped structures occurring between the neural arches of the vertebræ.

Mr Smith-Woodward observes that a gradual advance in the degree of calcification of the axial skeleton may be observed as we trace the members of the order from the Palæozoic upwards, the oldest forms not having the notochord differentiated into distinct vertebral centra, of which we find the first complete types in the Lower Liassic *Palæospinax*. Here, however, the centra merely assume the form of double cones, only very slight traces of the peripheral calcifications necessary to form the biconcave centra of the later types being visible. In the Lower Kimeridgian lithographic stone of the Continent, centra of the complete *asterospondylic* type are first met with.

The same authority mentions that the Palæozic types are, as a rule, characterised by the great development of the exoskeleton, although a few forms like *Pleuracanthus* appear to have had naked bodies. These early dermal structures are also noticeable for their elaborate sculpture, this being equally developed on the dermal granules (shagreen), and on the fin and cephalic spines. Smooth fin-spines appear to be very rare in the Palæozoic, and it is not till we reach the Upper Trias and Lias that spines completely covered with smooth ganoine are met with.

In regard to the teeth, Mr Woodward observes that "pointed teeth and obtuse teeth occur among the earliest Elasmobranchs; but the former as well as the latter are firmly articulated together, and must always have formed part of a dentition in which several series were functional. Though the teeth of *Cladodus* and *Diplodus* [*Pleuracanthus*] are as sharply pointed as those of most recent Sharks, the piercing crown is placed upon a broad horizontally-expanded base, permitting of a considerable amount of interlocking between one tooth and another—an arrangement most nearly paralleled in the surviving *Chlamydoselache*. It is evident, indeed, that all the modern types of dentition, in which not more than one or two series of teeth are simultaneously functional, are highly specialised modifications of this primitive arrangement; and the change results from the deepening and lateral compression of the root of each tooth, rendering its base of support less fixed, and often not permitting its coming into use until after attaining the summit or passing the outer side of the jaw-cartilage.

"With regard to the disposition of the teeth in the mouth as a whole, the modern Rays—most *Scylliidæ* and *Chlamydoselache*—may be looked upon as retaining the most primitive arrangement. In the predaceous Sharks there has been a tendency towards the relative enlargement of the prehensile teeth upon the symphysis; while

in the Cestraciont Sharks the symphysial teeth have become small though prehensile, and the lateral teeth well adapted for trituration. The former arrangement is particularly characteristic of modern times; the latter, it is interesting to note, attained its maximum of specialisation so long ago as the Carboniferous period. In many early Carboniferous genera the series of lateral crushing-teeth began in part to fuse into continuous plates (*Pleuroplax*); two of these plates often amalgamated (*Pœcilodus*); and in the most specialised of these Cochliodonts (*e.g.*, *Deltoptychius*), all traces of the boundaries of the original components of the dental plates became obliterated."

Suborder 1. Ichthyotomi.—This name was proposed by Professor Cope for a group of primitive Elasmobranchs, ranging from the Devonian to the Permian, but perhaps also surviving to the Trias, and showing the following characteristic features. The endoskeleton has granular calcifications extending equally throughout the cartilage; the notochord in most, or all, cases is not constricted to form distinct vertebræ; and the calcification of its sheath in the precaudal region does not extend beyond that very incomplete stage to which the term *rhachitomous* has been applied—the explanation of which is given below under the head of the Labyrinthodont Amphibians. The neural and hæmal spines of the vertebræ are long and slender, and no intercalary cartilages are developed. Finally, the pectoral fins have a long segmented axis of the archipterygial type (fig. 850).

It may be mentioned here that Dr Koken is indisposed to admit the right of the Ichthyotomi to form a group of equal rank, with that embracing all other Elasmobranchs; since he regards the primitive features exhibited by the vertebral column, and the nature of the caudal fin, as only one degree removed from those found in certain Selachii. This writer, indeed, regards the *Pleuracanthidæ* and *Cladodontidæ* as so closely allied to the *Notidanidæ* and *Cestraciontidæ* (*Hybodontidæ*) that he would class the whole of these families in a single group, for which he proposes the name *Proselachii*, and in which the *Cochliodontidæ* should perhaps also be included. So far as regards the slight importance from a classificatory point of view of the imperfect calcification of the vertebral column, Dr Koken's views are in harmony with those adopted below in the classification of the Labyrinthodont Amphibia.

Family Pleuracanthidæ.—In this family the body is slender and somewhat depressed; the mouth differs from that of all the Selachii in being terminal; while the caudal fin is diphycercal. There is a long and low continuous dorsal fin; while the pectoral fin has a biserial arrangement of rays somewhat after the fashion of *Ceratodus*. The type genus *Pleuracanthus* has received an almost bewildering number of names, of which it will suffice to mention *Diplodus*, *Orthacanthus*, *Xenacanthus*, and *Didymodus;* some of

these, as their terminations indicate, having been applied to spines, and others to teeth.

Recent discoveries have enabled us to attain to a nearly complete knowledge of the anatomy of this remarkable genus, and a restoration by M. Brongniart of one of the species is shown in the accompanying woodcut. The skin was quite naked; the body elongate, and the snout obtuse. The teeth have a thick and depressed root, with a crown formed by two unequal corners diverging like a V, with a small denticle at the base of the two, and not unfrequently a minute flattened mammilla posteriorly. In the male the pelvic fins carry a robust "clasper." At the top of the head there was a large barbed spine (fig. 852, 1), with a double row of serrations, and, according to the restoration (fig. 850), supporting a

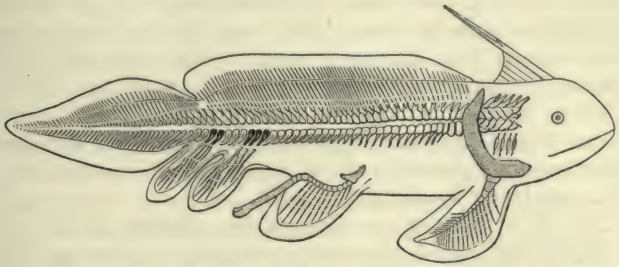

Fig. 850.—Restoration of the skeleton of *Pleuracanthus Gaudryi*; from the Carboniferous of France, reduced. (After Brongniart.)

cephalic fin. In the skull, according to Dr Koken, there was a distinct hyomandibular, but the palatopterygoid bar had a direct connection with the postorbital process of the cranium, as in *Notidanus*. Dr Koken would slightly modify the structure of the pectoral fin from that given in fig. 850. The dorsal fin is of great length, extending backwards as far as the diphycercal caudal, from which it is separated by a deep notch. According to M. Brongniart's restoration the anal fin was double, and its two divisions had a structure curiously like that of limbs; Dr Koken considers, however, that the restoration is incorrect in this particular. Specimens of the figured species attain a length of more than a yard.

In time this genus extends from the Carboniferous to the Lower Permian; while in space its range embraces both Europe and North America. *Chondrenchelys*, from the Lower Carboniferous of Dumfriesshire, which is provisionally referred to the same family, has no cephalic spine. Detached teeth from the Keuper of Somerset, described under the name of *Diplodus*, apparently indicate the survival of a form allied to *Pleuracanthus* in the Triassic period.

Family Cladodontidæ.—The second family of this suborder is too imperfectly known to admit of definition; but it appears that in the type genus the pectoral fin had only one series of rays, and was thus intermediate between that of *Pleuracanthus* and the fins of the Selachii. The type genus *Cladodus* had a broad and depressed

head, with the teeth arranged in numerous rows. The crowns of these teeth present some resemblance to those of the Selachian *Hybodus* (fig. 865); consisting of one large cone, flanked on either side by one or more smaller cones, of which the outermost is generally the largest. This genus is exclusively Carboniferous, and occurs both in Europe and North America; a large number of species being known. *Dicentrodus*, of the Scottish Carboniferous, is distinguished by the teeth having only a single lateral cone developed on one side. *Phœbodus*, of the Devonian of Iowa, is an allied genus, with the lateral cones of the teeth at least as large as the middle cone; while in *Lambdodus*, of the North American Palæozoic, these lateral cones are totally wanting. In *Dicrenodus*, of the Carboniferous of both Europe and North America, we have a modification of the Cladodont tooth, in which the central cone is compressed, with the cutting-edges serrated; while the lateral cones may either be two in number, or absent. Finally, the North American Palæozoic genus *Hypocladodus* differs from the preceding by the absence of serrations on the edges of the central cone; the lateral cones being invariably absent.

Suborder 2. Selachii.—The existing Sharks, Rays, and their allies are characterised by the endoskeleton being, as a general rule, only superficially calcified; while, except in some of the earlier forms, the notochord is constricted at the centre of each vertebra. The neural and hæmal arches of the vertebræ are short and stout; and intercalary cartilages are nearly always developed. The pectoral fin (fig. 846) has not a segmented axis, being of the ichthyopterygial type; and the axis of the pelvic fin of the male is produced into the so-called "clasper," which is connected with reproduction. Some of the other features of this suborder have been already mentioned at the commencement of this chapter. The Selachians may be divided into two sections, according to the structure of the vertebral centra. In the one the anal fin disappears, and there is a tendency to the depression of the body and the enlargement of the pectoral fins, but there is no diminution in the size of the spiracle, and the vertebræ, when fully developed, are of the type known as *tectospondylic*. In the other section the anal fin persists; the shape of the body is always rounded—not even excessively flattened in the *Scilliidæ;* the spiracle tends to abort, and may be almost or totally absent in the most specialised forms; while the fully developed vertebræ are of the type known as *asterospondylic*. The type of vertebral centra known as *cyclospondylic* occurs in the immature condition of both sections.

Section a. Tectospondyli.—In this section the vertebral centra, when fully calcified, have the concentric laminæ predominating over those that radiate from the centre. The anal fin is invariably want-

ing; while specialisation shows itself in the depression of the body and the enlargement of the pectoral fins—the spiracles being always retained. This section includes the Spiny Dog-fishes, Saw-fishes, Eagle-rays, and Rays.

Family Spinacidæ.—In this family, which includes the existing Spiny Dog-fishes (fig. 849), we have generalised forms, with the body more or less rounded, and but slightly depressed. The teeth are pointed; the pectoral fins are devoid of a notch at their root, and are not expanded anteriorly; while the gills are small and lateral, and the spiracles large. One fossil species referred to the existing Mediterranean genus *Centrina* has been recorded from the Pliocene of Italy; but this determination is not absolutely certain. *Acanthias* (fig. 849), of which two species are found at the present day in the temperate seas of both hemispheres, occurs in the Chalk of the Lebanon, and also in the Miocene of Würtemberg. Another fossil form from the Lebanon has been referred to the existing genus *Centrophorus*, but it may perhaps belong to *Acanthias*. The existing genus *Spinax* has been recorded from the Italian Pliocene. With *Scymnus* we come to another existing genus, differing from all those that precede by the absence of fin-spines. It occurs fossil in the Pliocene of Italy, which has also yielded remains referred to the allied *Echinorhinus*.

Family Petalodontidæ.—The Petalodonts form a family exclusively Carboniferous, presenting the following characters. The body was somewhat depressed, while the pectoral fins were large, and produced forwards in the direction of the head after the manner of the Rays. The teeth (figs. 851, 852) formed a close pavement in the mouth, and are compressed from before backwards, with the crown more or less bent backwards, and either blunt and obtuse, or with a cutting-edge, the root being often large. In the genus *Janassa* (*Climaxodus* or *Strigilina*), which is common to Europe and North America, the teeth (fig. 851) are so thickened and reflected, that the complete series forms an almost entirely triturating surface. These teeth are arranged in three chief rows, as in the figure, which gradually diminish in size anteriorly, and are flanked by one or more smaller rows of less thickened teeth. The body is covered with fine shagreen. The North American *Fissodus* has the margin of the crowns of the teeth cleft into two or three points; while in *Petalorhynchus*,

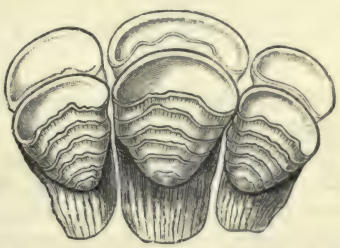

Fig. 851.—Posterior aspect of some of the central teeth of *Janassa linguæformis*; from the English Carboniferous.

which is found both in Europe and North America, the teeth are of the same general type, but have more compressed crowns, with long undivided roots. Again, in *Petalodus*, which has the same distribution as the preceding, the teeth (fig. 852, 4) are much elongated transversely, and compressed from before backwards—the crown being petal-shaped, with a smooth or slightly crenulated cutting-edge. The nature of the arrangement of the entire series is, however, unknown. The teeth of *Ctenoptychius* (fig. 852, 6) are distinguished by the coarser denticulation of their cutting-edge—those of *Callopristodus*

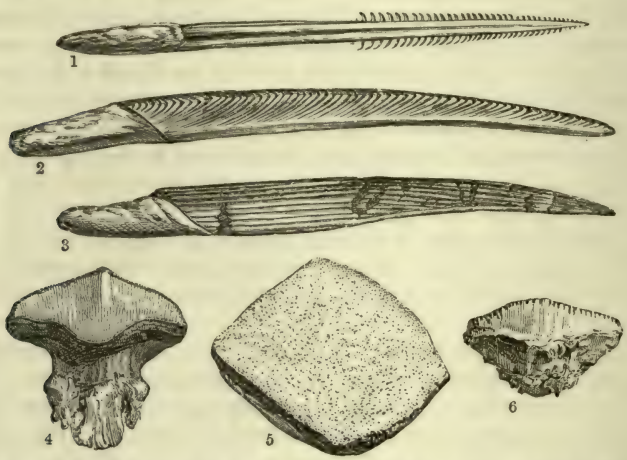

Fig. 852.—Spines and teeth of Carboniferous Elasmobranchei. 1, Nuchal spine of *Pleuracanthus lævissimus;* 2, Fin-spine of *Gyracanthus;* 3, Do. of *Sphenacanthus;* 4, Tooth of *Petalodus acuminatus*, seen from the side; 5, Do. of *Psammodus*, seen from above; 6, Do. of *Ctenoptychius.* 1–3 are reduced.

differing from the latter by the absence of enamel-folds at the base of the crown, and also by the nature of the root. It is probable that both these genera occur in North America as well as in Europe. In *Polyrhizodus* (*Dactylodus*), of both Europe and North America, the teeth are extremely stout, with low crowns, usually having a sharp cutting-edge devoid of crenulations, and a large root divided into a number of rootlets. Other allied genera from Europe are known as *Glossodus* and *Mesolophodus.*

Family Pristodontidæ.—This family is only known by the genus *Pristodus*, of the European Carboniferous, in which the crown of each tooth is thin, plate-like, and symmetrical, with hollows corresponding to elevations in the opposing tooth of the opposite jaw. It has been suggested that each jaw carried only a single tooth.

Family Squatinidæ.—With this family we come to a group represented at the present day by the Monkfish, of which the skele-

ton of the pectoral fin is shown in fig. 846 (p. 920). The body is depressed, with the mouth placed anteriorly; while the pectoral fins are much produced anteriorly, although unconnected with the head. The teeth are conical and pointed; and the dorsal fins are without spine, and placed on the tail. The only known genus is *Squatina* (*Rhina*), which ranges from the Kimeridgian upwards to the present day; although some of the fossil species have been described under other names, such as *Thaumas*. Beautifully preserved skeletons occur in the Lower Kimeridgian lithographic limestones of Bavaria, one of which is shown in the accompanying woodcut. Other species have been named from the Chalk of the Lebanon and of England, and also from the Miocene and Pliocene of the Continent; while detached teeth are found in the English Gault, the London Clay, and the Red Crag.

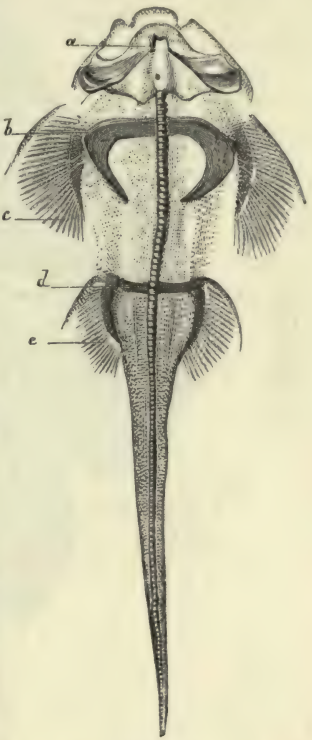

Fig. 853.—Ventral aspect of the skeleton of *Squatina speciosa*; from the Kimeridgian of Bavaria, two-thirds natural size. *a*, Mandible; *b*, Pectoral girdle; *c*, Pectoral fin; *d*, Pelvis; *e*, Pelvic fin.

Family Pristidæ.—In the true Saw-fishes the body is scarcely depressed, the pectoral fins are not much expanded, and the gill-slits are placed inferiorly. The most characteristic feature is, however, the so-called "saw," which is a long and flat calcified prolongation of the snout, armed with a series of large pointed teeth on either border. Remains of the single existing genus *Pristis* occur in the Middle Eocene of Barton and Bracklesham; in the Middle and Lower Eocene and Micoene of the Continent; and the Eocene and Upper Cretaceous of North America. *Propristis*, from the Eocene of Egypt, is said to differ by the absence of calcification in that part of the "saw" which supports the teeth; *Amblypristis*, of the same beds, has shorter and broader teeth than *Pristis*; while *Sclerorhynchus*, which may belong to the *Pristiophoridæ*, differs in the structure of the "saw," and the small size of the rostral teeth. The latter family, which has lateral gill-slits, may be represented in the Miocene of Würtemberg by a species of the existing *Pristiophorus*.

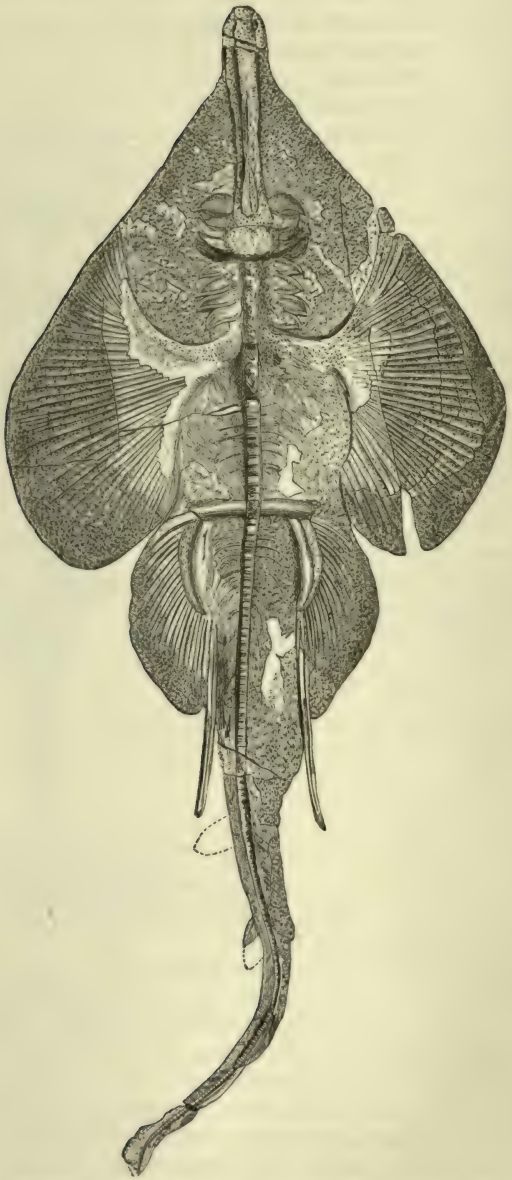

Fig. 854.—Skeleton of *Rhinobatis bugesiaca*; from the Kimeridgian of Bavaria, one-twelfth natural size. (After Zittel.)

Family Rhinobatidæ—With this family we come to Fishes to which the general term Rays may be applied; all of them are characterised by their extremely depressed bodies and the great development of the pectoral fins, so that the body proper with its fins is termed the "disk." The teeth always form a kind of pavement (figs. 856, 857). In the present family the tail is long and stout, with two well-developed dorsal fins; while there is also a caudal fin, with a longitudinal fold on either side. The disk is not excessively developed; the rayed portion of the pectoral fins not extending to the snout. The type-genus *Rhinobatis* (*Spathobatis*) is represented at the present day by about a dozen species, which inhabit the warmer seas, and attain huge dimensions. The snout is produced into a long rostrum, which is connected with the pectoral fin by a membranous expansion (fig. 854). The teeth are obtuse; and the dorsal fins are devoid of spines. In time this genus ranges from the Kimeridgian to the present day; species being recorded from the lithographic limestones of Bavaria (fig. 854) and France; from the Portlandian of France; the Chalk of the Lebanon and Italy; the Middle Eocene of Monte Bolca; the Miocene of Würtemberg; and other localities. The Australian *Trygonorhina*, which differs in the structure of the nasal valves, is said to occur in the Middle Eocene of Italy. Finally, the genera *Belemnobatis* and *Asterodermus*, respectively from the Kimeridgian of France and Bavaria, appear to connect the present with the following family.

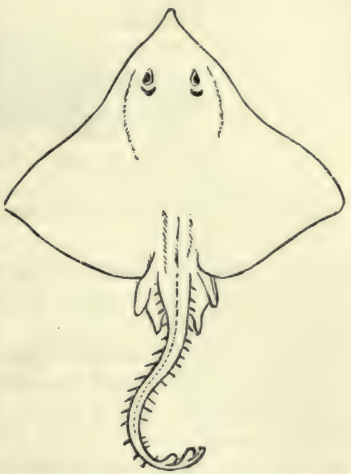

Fig. 855.—The Burton Skate (*Raia marginata*), one-sixth natural size. Recent. Britain. (After Gosse.)

Family Raiidæ.—In the true Rays or Skates (fig. 855) the disk is broad and rhomboidal, and usually has dermal rugosities; while the rayed portions of the pectoral fins extend to the comparatively short snout. The tail is also shorter than in the *Rhinobatidæ*, with a longitudinal fold; and the development of the median fin is subject to considerable variation. The type genus *Raia* (*Actinobatis*) has the tail very distinct from the body (fig. 855); the pectoral fins not reaching to the extremity of the snout; two dorsals, and either a rudimental or no caudal fin. The dentition (figs. 856, 857) often varies greatly in the two sexes; some or all of the teeth in the male being sharp, while

all those of the female are obtuse. Some of these Skates measure upwards of seven feet across the disk. In a fossil state this genus occurs in the Chalk of the Lebanon, and the Upper Eocene of Hampshire; and also in the Suffolk Crags and Italian Pliocene, where it is represented by the living *R. clavata* (figs. 856, 857). The extinct *Dynatobatis*, from the Tertiary of South America, is distinguished by the enormously expanded bases and the small spines

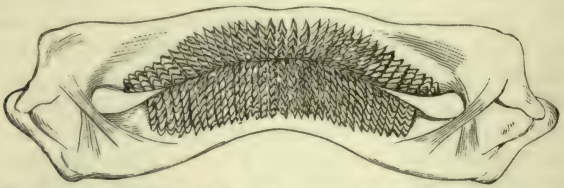

Fig. 856.—Front view of the jaws of the male Thornback Skate (*Raia clavata*). Reduced.

of the dermal tubercles with which the body is studded. *Acanthobatis*, from the Middle Miocene of France and Würtemberg, has tall dermal tubercles, with small bases, which often fuse together into

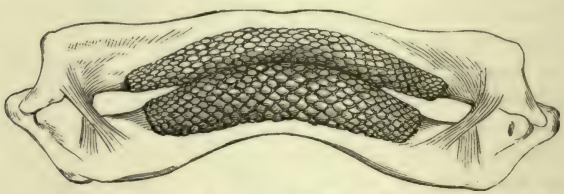

Fig. 857.—Front view of the jaws of the female Thornback Skate (*Raia clavata*). Reduced.

groups; while *Oncobatis* of the Pliocene of Idaho, which has these tubercles of a pentagonal form, may be identical with the type genus.

Family Torpedinidæ.—The Electric Rays have the disk broad and smooth; the rayed portion of the pectoral fins not continued beyond the base of the snout, and the median fins well developed. The peculiar electric organ is placed between the head and the pectoral fins. Extinct species of the existing genus *Torpedo* occur in the Middle Eocene of Monte Bolca, near Verona.

Family Psammodontidæ.—This extinct family is known only by portions of the dentition, so that its definition is at present impossible. It appears, however, from the parallelism of the mandibular rami that the body must have been depressed like that of the Rays. The teeth (fig. 852, 5) are of a flattened quadrangular form, with the root nearly as large as the crown, and were arranged in one or more longitudinal rows, which were arched antero-posteriorly with

some alternation of the teeth of adjacent rows. The genus *Copodus* has symmetrical teeth, with the postero-lateral angles of the root, and sometimes also of the crown, produced backwards; the teeth being narrowest in front, with the anterior margin usually either straight or convex. The crown surface when unworn is rugose, and marked by a more or less transverse line, which sometimes permits the two portions to be separated. This genus occurs in the Carboniferous of Europe. In the typical *Psammodus* the teeth (fig. 852, 5) are quadrangular, generally more or less oblong, but occasionally nearly square, with the root much thicker than the crown, from which it is easily separable; the surface of the crown being generally marked by transverse wrinkles. It is probable that the teeth were arranged in the jaws in four longitudinal rows. *Psammodus* is represented by a considerable number of species from the Carboniferous of both Europe and North America. Lastly, *Archæobatis*, from the Carboniferous of Indiana, is an allied form, with very large pavement-like teeth arranged in several rows, of which the under surfaces are somewhat excavated to fit the curvature of the jaws.

Family Myliobatidæ.—With the Eagle-rays we come to an existing family well represented in a fossil state as far down as the Lower Eocene; vertebræ from Cretaceous and Jurassic beds having been also referred to this family. The disk is very large, owing to the great development of the pectoral fins, which stop short at the sides of the head, but reappear at the extremity of the snout in the form of a small single or paired cephalic fin. The tail is extremely slender, and resembles a whip-lash; and the dentition, when present, forms a complete pavement. The type genus *Myliobatis* has the head free from the disk, and a single cephalic fin. The teeth are large, flat, and hexagonal, and are arranged in seven longitudinal rows; the middle row in the adult being extremely broad, while the lateral rows are lozenge-shaped (fig. 858). In the young the middle row of teeth is not larger than the lateral ones, and there is a gradual increase in the relative breadth of this row as the fish increases in age. The upper dental plate is extremely convex from before backwards, but the lower one is quite flat. In addition to the doubtful vertebræ mentioned above, this genus is known continuously from the Lower Eocene upwards, and has a wide distribution in space. Thus, in the Eocene, it is recorded from Europe, India, and

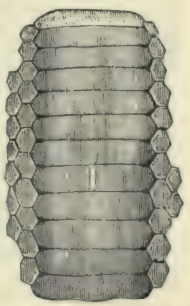

Fig. 858.—Part of the lower dental plate of *Myliobatis striata*, from the Middle Eocene of Brackle-sham, Sussex. Reduced. The second lateral rows of teeth are imperfect, and the third wanting.

North America; and it has also been described from the Tertiary of New Zealand. A very large number of specific names have been applied to the fossil forms, but Mr S. Woodward has shown that the number of valid species may be greatly reduced, since many of the characters on which they were founded are solely due to differences in the age of the specimens. In *Rhinoptera* (*Zygobates*), while the head is still free, there are two cephalic fins, and the teeth are arranged in five or more rows, of which the middle series and the adjacent pair are broad, while the one or two pairs on the borders form regular hexagons. This genus is known from the London Clay, the Eocene of South Carolina, the Swiss Miocene, and the English Crag, and is now represented by seven species from tropical and sub-tropical seas. The existing genus *Aëtobatis* is distinguished from the preceding by the teeth being arranged in only a single longitudinal row, which is often bent, and corresponds to the median row of *Myliobatis*. One species is found from the London Clay to the higher Eocene of Barton, and the genus is also represented in the Swiss Miocene. The existing genus *Ceratoptera* has no upper teeth.

In this family may be provisionally included the Cretaceous genus *Ptychodus*, which was long considered to be a Cestraciont Shark, but has been shown by Mr Smith-Woodward to be a Ray allied to *Myliobatis*. The connection between *Ptychodus* and the existing *Myliobatidæ* is shown by the genus *Apocopodon*, from the Upper Cretaceous of Brazil, which has teeth of an intermediate type; while some of the Eocene species of *Myliobatis* have teeth of nearly the same form as those of *Ptychodus*. The teeth of this genus (fig. 859) have quadrangular crowns, with the enamel of the central region thrown into a number of transverse folds, while the root is smaller and lower than the crown. The two sides of each jaw are parallel to one another, and the teeth are arranged in several parallel rows running from back to front, as is shown in the accompanying diagram (fig. 860). It will be seen, moreover, that each jaw has a single median series, composed of very small teeth in the upper, and of very large ones in the lower jaw; while on either side of this median row there is a series of teeth somewhat less large than the median row of the lower jaw. The five external rows gradually decrease in size towards the outer side of the jaws. A comparison

Fig. 859. — Oral and lateral views of the crown of a tooth of *Ptychodus polygyrus*, from the Upper Greensand of Regensburg. (After Zittel.)

with fig. 858 will show that the general plan of this arrangement of the teeth is essentially the same as in *Myliobatis*. This genus has a wide distribution, being found in the Upper Cretaceous of Europe, India, and North America.

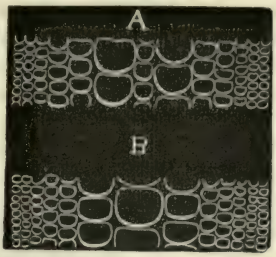

Fig. 860.—Diagram of the arrangement of the teeth in the upper (A) and lower (B) jaws of *Ptychodus decurrens*. (After S. Woodward.) Reduced.

Family Trygonidæ.—In this family the pectoral fins continue to the extremity of the muzzle, with which they are confluent. The tail is slender, and sharply distinguished from the disk; while the vertical fins are imperfect or absent, and may be replaced by serrated spines. There is some uncertainty as to the occurrence of *Trygon* in a fossil state, but it is probable that either this genus or the allied *Tæniura* date from the Middle Eocene of Monte Bolca, and remains referred to the former have been described from the Upper Cretaceous of New Zealand. The extinct *Xiphotrygon*, from the Eocene of Wyoming, is distinguished by its cuspidate teeth. Remains referable to the existing tropical genus *Urolophus* occur in the Middle Eocene of Italy, and perhaps in that of Belgium; while *Cyclobatis* is an extinct genus from the Cretaceous of the Lebanon.

Section B. Asterospondyli.—This section is distinguished from the last by having the radiating laminæ predominating over the concentric ones in the fully calcified vertebral centra, so that a section shows a star-like arrangement. The anal fin is always present; while specialisation does not tend to a flattening of the body, or to an expansion and forward growth of the pectoral fins, and the spiracles are small, and may disappear. This section comprises the true Sharks and the Dog-fishes.

All these fishes have elongated and subcylindrical bodies, and a strong tail, well adapted for swimming. The anterior, and very frequently all the teeth are formed on the type of a laterally compressed cone with trenchant edges, at the base of which two or more minor cones may be developed. In many cases, however, the hinder teeth have obtuse crowns, adapted for crushing. The two rami of the jaws are never parallel to one another, in consequence of which the teeth are always set in oblique rows (fig. 864), and never form the straight antero-posterior rows, like those occurring in the Rays (fig. 860). Sharks are carnivorous, and of active pelagic habits; and are most numerous in tropical seas, although they ascend tidal rivers, and are even found in an inland lake in the Fiji Islands.

This section may be divided into two series, in the first of which

there is but one dorsal fin, and the number of the gill-clefts exceeds five.

Family Notidanidæ.—The single family of this series is represented by the genera *Notidanus* and *Chlamydoselache*, both of which inhabit the warmer seas. The dorsal fin has no spine, and the teeth, of which several series are in use at the same time, have sharply pointed cusps. *Notidanus* (*Heptanchus*, *Hexanchus*) is readily

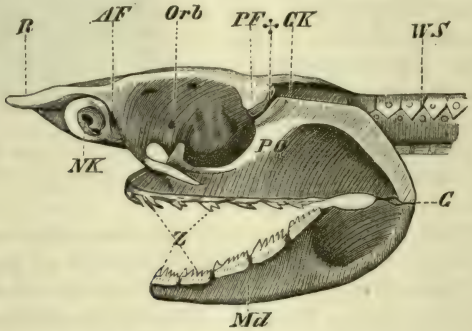

Fig. 861.—Left lateral view of the skull of *Notidanus*. Recent. Reduced. *R*, Rostrum; *AF*, *PF*, Pre- and postorbital processes; *Orb*, Orbit; *NK*, Nasal capsule; +, Articulation of palatopterygoid (*PQ*); *C*, Articulation of Meckel's cartilage (*Md*); *Z*, Teeth; *WS*, Vertebral column. (After Wiedersheim.)

characterised by the inferior position of the mouth and the peculiar form of the lateral teeth. These lateral teeth (figs. 861, 862) are comb-like, consisting of a series of compressed cones, inclined in one direction, and fixed upon an elongated base; the anterior cone being the largest, and frequently having cusps at the base of its anterior border. The lower teeth are more complex than the upper, and the anterior teeth in both jaws are simple and awl-shaped. The primitive position of this genus is shown by the persistent notochord and the characters of the skull (fig. 861). The latter approaches the so-called amphistylic type, differing from that of all other existing Selachians by the slenderness of the upper part of the hyoid arch, which does not support the palatopterygoid bar and mandible. The palatopterygoid is connected, however, with the cranium by a distinct facet articulating with the postorbital process. This structure is re-

Fig. 862.—Lower teeth of *Notidanus gigas*; from the Red Crag. The anterior cusps are worn away in the lower figure. (After Smith-Woodward.)

garded by Mr Smith-Woodward as but very slightly removed from the original primitive condition; *Cestracion*, in which the hyomandibular becomes distinctly differentiated, being a step in advance. In time this genus is definitely known to range from the Middle Jurassic of the Oxford Clay to the present day; it has indeed been recorded from the Lias, but the determination is more than doubtful. Nearly all the described species are European, but one has been recorded from the Tertiary of New Zealand. Some of the fossil teeth show signs of wear at their summits, and it thus seems that they must have been firmly implanted in the jaws like those of the Hybodonts; specialisation having apparently tended to produce a loose dental articulation throughout the section. The genus *Chlamydoselache* has a terminal mouth, with lateral teeth similar in both jaws, and consisting of three slender cones separated by smaller cusps; the notochord being partly calcified. This genus is now known by a single living species from the Japanese seas, but teeth from the Pliocene of Tuscany have been referred to it. It will be observed from the figure that the mandibular articulation of *Notidanus* is placed far behind the cranium proper, and it is noteworthy that a similar condition obtains in *Pleuracanthus* among the Ichthyotomi.

Family Cochliodontidæ.—With this family we enter the second series of the section, in which there are two dorsal fins and five gill-clefts. The present extinct family is an ill-defined one, apparently allied to the *Cestraciontidæ*, but with a more specialised dentition. The dentition is formed from that of the *Cestraciontidæ* (*infra*) by the welding of at least one of the oblique transverse rows of teeth encircling each ramus of the jaws into a continuous curved plate (fig. 863), which may have either a smooth crown-surface, or may be marked, as in the figured example, by grooves and ridges, indicating its compound origin. These dental plates grow by additions to their inner borders, while the outer borders are usually involuted. The dorsal fins were provided with spines. This family comprises a number of genera from the Carboniferous, only some of which can be very briefly noticed in this work. The one most imperfectly known is *Helodus*, from the English Carboniferous, which appears allied to the next, but does not seem to have had the teeth welded into plates, and therefore differs from the accepted definition of the family. *Pleuroplax* (*Pleurodus*) and *Psephodus* are more typical forms, the latter occurring both in Europe and North America. The dental plates of *Psephodus* form at least one series of smooth curved teeth, without coronal ridges or involution of the outer border; and there were also smaller rows of lateral teeth, as well as some prehensile teeth at the extremities of the jaws. *Sandalodus* is known by the huge dental plates, which are of an elongated trian-

gular shape, with the outer border slightly involuted, and an undulating coronal contour in the upper jaw; the genus occurring in Europe and the United States. Other genera which can be merely mentioned are *Tomodus*, *Xystrodus*, *Deltodus*, and *Pœcilodus;* the three last being common to Europe and North America. Teeth referred to *Pœcilodus*, and to the above-mentioned genus *Psephodus*, have also been described from the Carboniferous of Northern India; and the teeth from the same beds described under the name of *Helodopsis* are likewise referable to the present family. In the type genus *Cochliodus*, of Europe and the United States, there are two pairs of dental plates in the mandible (fig. 863), in which the outer border is much involuted. The posterior plate is elongated anteroposteriorly, and has its anterior and posterior borders converging outwardly, and a prominent oblique ridge, likewise narrowing in the same direction, in the middle of the crown. The anterior plate is narrow from before backwards, with a ridge on the hinder border of its crown resembling the median ridge of the larger plate. The remaining genera of this family are *Streblodus*, *Deltoptychius*, *Diplacodus*, and *Cyrtonodus*, of which the two last are doubtfully entitled to distinction; while other names have been applied to detached anterior teeth.

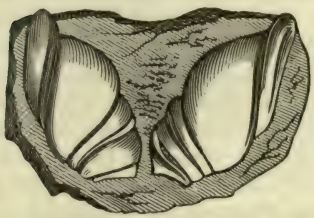

Fig. 863.—Lower dental plates of *Cochliodus contortus;* from the Carboniferous of Armagh. One-half natural size. The specimen is viewed from the anterior aspect, and the white line on the left side shows the division of the two plates.

Family Cestraciontidæ.—This family, which may be taken to include the *Orodontidæ* and *Hybodontidæ* of many writers, is represented by a considerable number of genera ranging from the Carboniferous to the present day; all the existing species being included in the type genus *Cestracion*, of which the upper dentition is shown in fig. 864. The family is characterised by the presence of a spine to each dorsal fin, of which the first is placed immediately above the interval between the pectoral and pelvic fins. The teeth are generally more or less obtuse, with several series in use at the same time, and those of each oblique series never fused into continuous plates. One of the oldest genera is *Orodus* (more correctly *Oreodus*), of the Carboniferous of Europe and the United States, in which the teeth are of the general type of those of *Hybodus*, and are only regarded by Mr S. Woodward as entitled to separation on account of the absence of other associated remains which are characteristic of the Mesozoic genus. It is probable that some of the dorsal fin-spines originally described under the name of *Ctenacanthus* belong to

Orodus. Most of these spines (fig. 852, 2) are, however, referable to the allied Carboniferous genus *Sphenacanthus;* and they are characterised by their ornamentation of robust longitudinal ridges,

Fig. 864.—Upper jaw of the Port Jackson Shark (*Cestracion Philippi*). One-half natural size. (After Owen.)

which are partly nodose. Other Carboniferous genera are *Campodus*, *Diclitodus*, and *Tristychius*, some of which have several synonyms. In the Thuringian Permian this family is represented by the genus *Wodnika*, in which the teeth have large and smooth crowns well

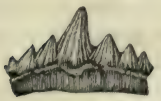

Fig. 865.—Tooth of *Hybodus raricostatus;* from the Lias of Dorsetshire. (After S. Woodward.)

Fig. 866.—Imperfect fin-spine of *Hybodus* (*cf*) *basanus;* from the Lower Cretaceous. Reduced.

adapted for crushing; while in the Muschelkalk, or Middle Trias, we have the imperfectly known *Palæobatis*, with teeth very like those of *Asteracanthus*. With the genus *Hybodus*, ranging from the Muschelkalk to the Lower Greensand of Europe, we come to a type which is now almost as well known to us as existing Sharks, owing

to the beautiful preservation of many of the specimens from the Lias, in which deposits these fishes were abundant. Many of the numerous species attained very large dimensions; and the genus may be defined by the following characters. The teeth (fig. 865) are conical or cuspidate, the crown being more or less striated, with one main cone, flanked by one or more lateral cones, and the root being more or less depressed. The teeth at the symphysis are large and few in number; while the fin-spines (fig. 866) are longitudinally grooved and ridged, with two rows of denticles placed near the posterior borders. The most remarkable feature is, however, the presence of two large hook-like spines immediately behind each orbit, which have been described under the name of *Sphenonchus*. The notochord is persistent.

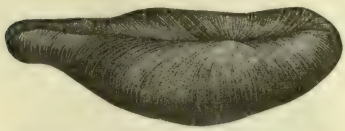

Fig. 867.—Tooth of *Acrodus nobilis*, from the Lower Lias of Lyme-Regis.

Specimens of the Lower Liassic *H. Delabechei* show the whole of the dentition *in situ*; and it appears from these that there was no median symphysial row of mandibular teeth, but that there were ten transverse rows of lower teeth, with five teeth in each row, while the number of rows in the upper jaw was either nine or ten. In the later forms, such as *H. basanus* of the Wealden, the teeth differ from those of the typical Liassic forms by the taller, compressed, and nearly smooth crowns, and Mr Woodward suggests that it may eventually be advisable to refer these types to a distinct genus. The orbital hooks found in the Oxford and Kimeridge clay indicate fishes of very large dimensions.

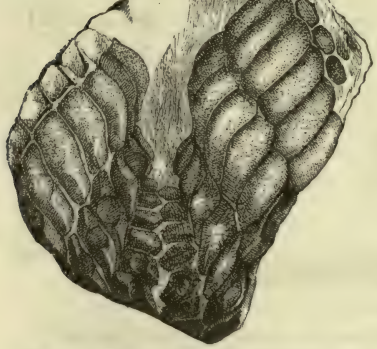

Fig. 868.—Part of the palate of *Asteracanthus ornatissimus*, from the Great Oolite of Caen. Reduced. (After Owen.)

The genus *Acrodus* is closely allied to the preceding; but the teeth (fig. 867) are non-cuspidate and more rounded. This genus is abundant in the Lias, where it is represented by the large *A. nobilis*, which is the type; but it also extends downwards to the Muschelkalk, and ranges upwards as high as the Chalk. The majority of the species are European, but the genus has also been recorded from the Cretaceous of North America, as well as from certain beds in that country which have been stated to be Miocene.

Asteracanthus (*Strophodus*) agrees with *Hybodus* in the persistent notochord and the presence of orbital spines, but differs in the characters of the fin-spines and teeth (figs. 868, 869). The principal teeth form irregular rhomboids, with slightly arched and flattened crowns, marked by a reticulate ornamentation—the symphysial teeth being large, few, and simple. The fin-spines are marked by stellate tubercles, which are sometimes fused, and have two posterior mesial series of denticles. The type species (fig. 868) is of great size, and occurs typically in the Great Oolite of the Continent and England, but ranges upwards to the Kimeridge Clay, and thus presents a remarkable instance of persistence. This genus is also represented in the Purbeck. Other extinct genera are *Palæospinax*, from the Lias, and *Synechodus* from the English Chalk, both of which have teeth closely resembling those of *Hybodus;* but the fin-spines, at least in the former, were smooth, like those of *Cestracion*. The Cretaceous genus is the more specialised, and approximates in cranial structure to *Notidanus*, the palatopterygoid articulating directly with the cranium. Finally, the existing genus *Cestracion* (in which may be included forms described under the names of *Gyropleurodus* and *Drepanophorus*) occurs in Europe from the Kimeridgian of Bavaria to the London Clay, and is now represented by four species in the Australian and Japanese seas. This is a specialised genus differing from *Asteracanthus* by the absence of orbital spines, the numerous and small symphysial teeth (fig. 864), the smooth fin-spines, and the full calcification of the vertebral column.

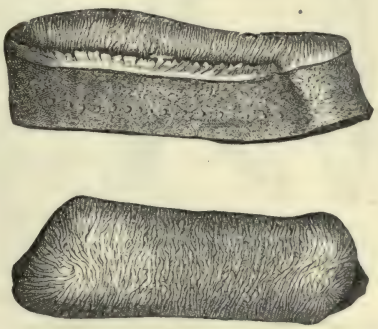

Fig. 869.—Lateral and oral surfaces of a tooth of *Asteracanthus ornatissimus*, from the Corallian of the Continent. (After Zittel.)

Family Scyllidæ.—This is a family of small extent, and most of the members of which are of relatively small dimensions. The dorsal fins have no spines, and the first is placed above or behind the pelvic fin; while the teeth are small and cuspidate, generally several series being simultaneously in use. The living forms are commonly known as Dog-fishes. *Palæoscyllium*, of the Lower Kimeridgian of Bavaria, seems to be allied to the existing *Ginglymostoma* and *Scyllium*. *Scylliodus*, of the English Chalk, is an imperfectly known form with teeth like *Scyllium*, but with vertebræ approximating to *Lamna*. *Scyllium* itself is represented in the Cretaceous of

the Lebanon and in the Continental Miocene; while allied extinct genera are *Pristiurus*, from the Lower Kimeridgian of Bavaria, and *Mesitia*, from the Lebanon beds. Finally, the existing *Chiloscyllium* occurs in the Miocene of Würtemberg; while *Ginglymostoma*, of which some of the existing species attain a length of 12 feet, is represented in the Eocene of Alabama.

Family Lamnidæ.—This family comprises the largest of the Sharks, and is characterised by having the first dorsal fin placed above the interval between the pectoral and pelvic fins, and without a spine. The teeth are acuminate, and when fully adult are solid throughout. The earliest form which has been referred to this family is *Carcharopsis*, known by detached teeth from the Carboniferous of Europe and North America. The type genus *Lamna*, in which *Otodus* may be included, comprises the existing Porbeagles, and has large lanceolate teeth (fig. 870) with basal cusps, but without marginal serrations. Teeth agreeing with those of existing forms in their general contour are found in Europe from the Lower Miocene (fig. 870) upwards, the so-called *L. acuminata*, from the Chalk, belonging, however, to the next genus. In another group of this genus, formerly known as *Otodus*, the teeth (fig. 871) are distinguished by the great compression of the crown, the large basal cusps, and the shortness of the root. Teeth of this type occur in Europe from the Gault to the London Clay, and are also represented in the Upper Cretaceous of Southern India and New Zealand. The nearly allied but extinct genus *Oxyrhina* is characterised by the still greater compression of

Fig. 870.—Tooth of *Lamna cuspidata*, from the Lower Miocene (Oligocene) of Germany. (After Zittel.)

Fig. 871.—Tooth of *Lamna appendiculata*, from the English Chalk.

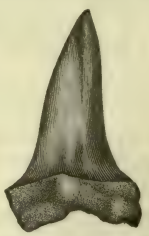

Fig. 872.—Tooth of *Oxyrhina plicatilis*, from the Hungarian Miocene.

the crowns of the teeth (fig. 872), which are generally devoid of basal cusps. It has been recorded from the Jurassic, and occurs abundantly in the Chalk of Europe, India, and New Zealand, and is also represented in the European Miocene. Teeth from the Upper Cretaceous of Europe and India, differing from those of *Lamna* by the nearly circular section of their crowns, have been referred to the existing genus *Odontaspis;* but Mr S. Woodward considers that they belong to a genus from the Cretaceous of the Lebanon, originally described under the preoccupied name of *Rhinognathus*, but now known as *Scapanorhynchus*. *Odontaspis* itself occurs in the Eocene. Teeth of a long and slender type, from the Upper Jurassic and Lower Cretaceous, have been described under

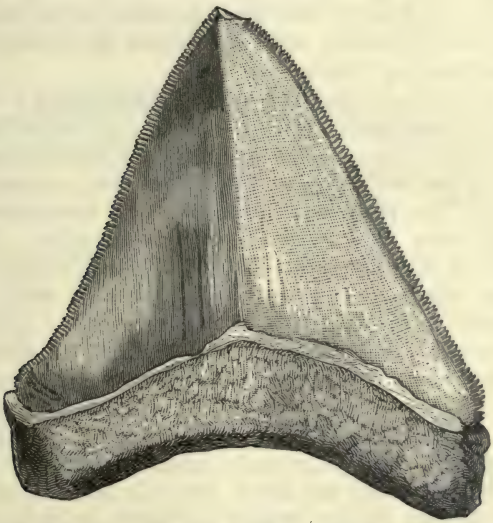

Fig. 873.—Tooth of *Carcharodon megalodon*, from the Miocene of Malta. (After Zittel.)

the name of *Sphenodus*, now changed to *Orthacodus*. Other teeth, from the Continental Miocene, have been referred to the existing genus *Alopecias* or "Threshers." With *Carcharodon* we come to Sharks of enormous size, characterised by their large, flat, and regularly triangular teeth (fig. 873), in which the edges are serrated, and there are no basal cusps. The one existing species attains a length of 40 feet, and has teeth measuring a little over 2 inches along the margins, with a basal width of 1.8 inches. It occurs fossil in the Pliocene of Europe. In the Red Crag, and also at the bottom of the Pacific, teeth are, however, found in which the corresponding dimensions are 5 and 4 inches, and thus indicate enormous indi-

viduals. Smaller teeth (fig. 873) also occur commonly in the Miocene of Malta, the Tertiary of New Zealand, and still smaller forms (fig. 874) in the Lower Miocene and Eocene of the Continent; and the genus is also represented in the Pliocene of Burma. Its earliest representative is, however, *C. longidens*, from beds which appear to be of the age of the Maastricht or topmost Cretaceous. Small compressed and triangular teeth, usually with serrated edges, from the Chalk of Europe and India, to which the name *Corax* has been applied, probably indicate Sharks allied to *Carcharodon*, although in external contour they approximate to the teeth of the next family: they have, however, solid crowns. The genus *Cetorhinus* (*Selache*), now represented by the huge Basking Shark, dates from the Pliocene.

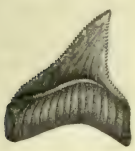

Fig. 874.—Tooth of *Carcharodon productus*, from the Lower Miocene of the Continent. Reduced.

Family Carchariidæ.—The last family we have to mention is distinguished from the preceding by the presence of a nictating membrane to the eye, and also by the hollow crowns of the teeth. It is unknown before the Upper Cretaceous, and is dominant at the present day. The teeth have triangular and compressed crowns, usually with more or less distinctly serrated edges. The genus *Hemipristis*, of the Upper Chalk and Lower Tertiary, is characterised by its tall lanceolate teeth, the crowns of which have both edges coarsely serrated, except at their summits. The existing genus *Galeocerdo* is first recorded from the topmost Cretaceous of Holland, and occurs throughout the European and American Tertiaries from the Eocene upwards; the existing forms being known as "Topes." *Carcharias*, including the well-known Blue Shark, has small and generally triangular teeth, those of the upper being very different from those of the lower jaw. It may be divided into several groups from the structure of the teeth, which in some forms have smooth edges. It first occurs in the London Clay, and is thence found throughout the European Tertiary series; it has also been recorded from the Egyptian Eocene, and is found in the fresh-water Pliocene Siwaliks of north-western India. The strange Hammer-headed Shark, the only representative of the genus *Sphyrna* (*Zygæna*), has teeth so closely resembling those of *Carcharias* that it is almost impossible to distinguish detached specimens. It appears, however, that there is sufficient evidence to prove the existence of a species of the former genus in the Miocene of Europe and of the United States.

Ichthyodorulites.—In conclusion, a brief notice may be given of a few of the numerous genera founded upon the so-called "ichthyodorulites" or spines, of which the serial position cannot at

present be determined, and several of which are probably referable to the Chimeroidei. The earliest of these is *Onchus* (fig. 875, A), from the Silurian bone-bed of Ludlow, to which genus may also belong the dermal denticules (*ibid.*, B) described under the name of

Fig. 875.—Spine (A) of *Onchus tenuistriatus*, and (B) Dermal plates of *Thelodus*; from the Silurian of Ludlow.

Thelodus. In the Devonian of North America, and also in the Upper Silurian or Devonian of Bohemia, large spines have been described under the name of *Machæracanthus* (fig. 876), which probably belonged to the dorsal fins. *Gyracanthus* is based on

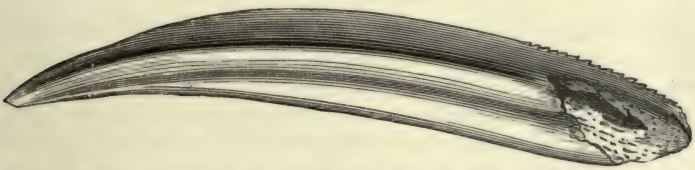

Fig. 876.—Fin-spine of *Machæracanthus major*; from the Devonian of North America. One-half natural size. (After Newberry.)

unsymmetrical spines (fig. 852, 2), which, it has been suggested, may belong to the pectoral fins. Other Carboniferous specimens have been named *Lophacanthus* and *Oracanthus* (England), *Euacanthus* (Russia), *Xystracanthus* (North America and India), and *Thaumatacanthus* (India). The spines described as *Oracanthus* are now known to belong to the head of a Selachian, and not, as at first supposed, to the tail of a Placodermic Ganoid. It will be unnecessary to mention a number of other types from various deposits; but we must not conclude without referring to the remarkable specimens (fig. 877) from the Carboniferous of North America and Australia, to which the name *Edestus* has been given. These have a highly curved axis, bearing compressed lancet-like teeth, with serrated edges

Fig. 877.—Part of (? caudal) spine of *Edestus vorax*; from the Carboniferous of North America. One-half natural size. (After Newberry.)

either on the convex or on both borders. It is suggested that they may have been carried on prominences in the caudal region. And after describing the best preserved remains of this genus, Dr Newberry concludes as follows: "Hence, until further light shall be thrown upon the interesting question of the homologies and functions of [the remains of] *Edestus*, we may regard them as the post-dorsal spines of large cartilaginous fishes, of which the other parts are yet unknown, and may suppose that they were used for attack and defence, like the spines of *Trygon* or *Acanthurus*."

Spines of similar type from the Carboniferous of Russia, originally described as *Edestus protopirata*, have been subsequently made the type of the genus *Protopirata*, although it is doubtful whether this term, having been first made a specific one, is admissible as a general one.

CHAPTER XLVIII.

CLASS PISCES—continued.

Orders Chimeroidei and Dipnoi.

Order III. Chimeroidei.—The Chimæroids are marine fishes, regarded by some writers as a suborder of Elasmobranchei; but although they resemble Sharks in external contour, in the presence of "claspers" on the pelvic fins of the male, and in the structure of the egg-capsules, yet they present such important differences as to indicate the propriety of referring them to a distinct order. The skeleton is entirely cartilaginous, and the vertebral column only imperfectly segmented; the notochord being surrounded by a series of cartilaginous rings, which may be partly calcified. The skin of the typical forms is usually quite naked in the adult, but in the young there is a row of small dermal ossifications on the back. The skull is movably articulated to the vertebral column, and has the hyomandibular fused with the palatopterygoid bar, and the latter firmly united to the cranium, with which the mandible consequently articulates without the intervention of a separate suspensorium—this arrangement being termed *autostylic.* The gill-clefts are four in number, and protected by a fold of skin containing a cartilaginous gill-cover; their communication with the exterior being effected by a single aperture. The mouth is always terminal; and in the recent forms each jaw carries one pair of molariform teeth, respectively attached to the palatopterygoid and Meckel's cartilage (mandible), with the addition of a smaller anterior pair of vomerine cutting-teeth in the upper jaw—all these teeth persisting throughout life. The fins are similar in structure and position to those of the Sharks; the first dorsal always carrying a strong spine, which articulates with the neural spines of the vertebræ, and is thus susceptible of motion. In the absence of a swim-bladder the Chimeroids, again, agree with the Elasmobranchs. There is a lateral line strengthened by cartilaginous rings. From the absence of any membrane bones, the

massive teeth, which are strictly comparable to those of the Dipnoi, constitute the whole of the solid part of the jaws.

This order may be regarded as in some respects connecting the Elasmobranchs with the Dipnoi—the autostylic cranium and the dentition being essentially Dipnoid. Chimæroids have existed from the Lias upwards, and not improbably date from the Devonian; while, as is usually the case, some of the extinct genera show much more generalised affinities than their existing representatives.

Family Squaloraiidæ.—The extinct genus *Squaloraia* was long regarded as an Elasmobranch of somewhat uncertain affinities; but according to the observations of Dr Traquair, it should find a place in the present order. In this genus, which is confined to the Lias, there is an elongated body; while the skull is produced into a long flat rostrum, and carries a basal pair of teeth separated at the symphysis, in advance of which are two small vomerine teeth of the normal Chimæroid type. Further, the skull of the male has a prehensile spine on the upper part of the snout, resembling in structure that found in *Ischyodus*. The "lateral line" agrees with that of other Chimæroids in being open, and protected by cartilaginous rings; while the skin appears to have been entirely naked. The vertebræ are of the Tectospondylic type of those of the Rays. The skull has been described as hyostylic, but Dr Traquair considers that this is due to crushing, and that it is really of the autostylic structure.

Family Chimæridæ.—Nearly all the remaining forms, from the Lias upwards, may apparently be included in this family, which is now represented by *Chimæra* and *Callorhynchus*. The teeth are of enormous size, those of opposite sides meeting in a median symphysis; and each tooth has one or more triturating ridges, or prominences, differing in appearance from the rest of the tooth, which may be conveniently termed *tritors*. The type genus *Chimæra* has the teeth adapted for cutting; those of the mandible being thin and plate-like, with one large median tritor, and two tritors near the anterior extremity, and an outer series in the form of dots; while the palatal tooth varies considerably in shape. This genus is represented at the present day by three species, and has also been recorded from the Pliocene of Italy and the Miocene of Bavaria. In *Elasmodectes* (*Elasmognathus*) of the English Chalk, the mandibular teeth are likewise of a cutting type, but without the median tritor. The extinct *Ischyodus*, which in England ranges from the Upper Jurassic to the Chalk, but has also been recorded from the Eocene of North America and the Cretaceous of New Zealand, appears to connect *Chimæra* with the next genus; the teeth being more adapted for crushing. The mandibular teeth are, indeed, more massive, and generally have two well-marked tritors externally to the large

median one; while there is a spine on the rostrum. *Edaphodon*, which ranges from the Lower Greensand to the Middle Eocene of Bracklesham, like the last genus, attains gigantic dimensions, but has its teeth adapted entirely for crushing. The mandibular tooth (fig. 878) is very massive, and has its symphysial surface (which in the preceding genera is narrow and grooved) very wide and quite flat, while there are two outer and one median tritors, as well as a terminal tritor which is not shown in the figure. Each palatal tooth is furnished with three tritors. Teeth of this genus are common in several Cretaceous and Tertiary deposits. *Elasmodus*, which is found in the Lower and Middle Eocene of England, appears to be

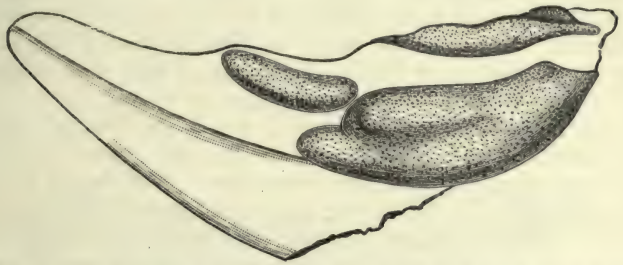

Fig. 878.—Inner surface of the right mandibular tooth of *Edaphodon gigas*; from the English Chalk. Reduced. (After Egerton.)

allied to the preceding genus; while in the existing *Callorhynchus* we apparently have the most specialised representative of the group with crushing teeth. The latter genus is represented by an existing species in the Southern seas, and by a fossil one from the Lower Cretaceous of New Zealand. The mandibular tooth is massive, with a narrow symphysis, and only a single tritor, representing the large median one of *Edaphodon*. Other European forms are *Ganodus*, from the Lower Jurassic of Stonesfield, in which the tritors of the mandibular tooth are confluent; and *Myriacanthus* (*Prognathodus* or *Metopacanthus*), of the Lower Lias of Dorsetshire, which is known both by the spines and the teeth. Its premaxillary teeth are chisel-like in shape. *Leptacanthus* of the Lias, and *Dipristis* of the Middle Miocene, are imperfectly known forms probably referable to this family. In North America the names *Eumylodus*, *Leptomylus*, *Byactinus*, *Diphrissa*, *Isotænia*, and *Sphageopœa* have been applied to Cretaceous forms, while a Miocene type has been called *Mylognathus*; but there is considerable doubt whether all these forms are really distinct from European genera.

As genera of which the family position is uncertain may be mentioned *Chimæropsis* from the Lower Kimeridgian of Bavaria, which differs from existing forms by its shagreen skin, and apparently also

by the presence of a remarkable spine-like tooth placed in front of the normal tooth of the mandible. The fin-spines of this genus approximate to those of the Elasmobranchian genus *Asteracanthus*. *Rhynchodes* from the Devonian of Ohio, and *Ptyctodus* from that of both Russia and Illinois, are genera founded upon teeth which their describers refer to this order. Some of the genera founded upon the evidence of detached fin-spines, a few of which are noticed in the preceding chapter, should perhaps also find a place among the Chimæroids.

Finally, the genus *Cœlorhynchus* may be mentioned in this connection. It was founded upon spines originally regarded as the rostra of Sword-fishes, but which are evidently of dermal origin, and are considered by Mr S. Woodward as being probably fin-spines of Chimæroids. These spines occur in the Chalk of England and Maastricht, in the Lower Eocene of England, Egypt, and India, and also in the Middle Eocene of Bracklesham in Sussex.

Order IV. Dipnoi.—The Dipnoi, which Dr Günther regards as a subdivision of the Ganoidei, are typically freshwater fishes, usually presenting the following characters: The body is covered with imbricating cycloidal scales, while the vertebral column is cartilaginous, and there are both anterior and posterior nostrils placed more or less within the mouth (fig. 881). The primitive cartilaginous cranium persists more or less completely, and, like that of the Chimæroids, is autostylic; cranial membrane bones are, however, always developed to a certain extent, and there are also splenial and articular bones in the mandible, while the cranium is immovably connected with the vertebral column. The palatopterygoid bar persists as the functional upper jaw, and, as in the living Chimæroids, carries a single pair of molariform teeth, while a corresponding pair of teeth are placed on the splenial and articular bones of the mandible. There is also a smaller pair of vomerine teeth; in advance of which there may be other minute teeth. The paired fins have a long, cartilaginous, jointed, median axis (fig. 845), and the tail may be either diphycercal or heterocercal. There are no functional branchiostegal rays; and the five or six cartilaginous branchial arches are more or less rudimentary, and their single aperture is closed by a gill-cover. The teeth agree with those of the Chimæroids in having no successors; but, from the presence of membrane bones, do not constitute the whole of the jaw.

In the structure of their skull the Dipnoi show affinities to Chimæroids, Ganoids, Teleosteans, and Amphibians; the autostylic feature connecting them with the former, and the double nares with the latter, in which the skull is also autostylic. The lungs are formed by the connection of the swim-bladder with the gullet by means of a duct, and these fishes can thus either breathe by means

of their gills in water, or by their lungs on land. In the existing African *Protopterus* there are external branchial tufts, like those of the young of the Amphibia. The structure of the pelvic girdle and limbs has been already noticed in the introductory chapter on the class; but it may be observed that although the skeleton is essentially cartilaginous, yet imperfect ossifications may occur in the neural spines of the vertebræ, as well as in the ribs and fin-rays. The scales may be either ganoid or cycloid.

That this order is essentially an old one, may be inferred not only from the widely scattered distribution of the three existing genera, and their paucity in species, and sometimes in individuals; but also from the generalised structure of its members, and the occurrence of one of the existing genera in the Trias of Europe, and the reputed Permian of North America.

Family Lepidosirenidæ.—This family is only known by two existing genera, and is characterised by the persistent chondrocranium, carrying a few large membrane bones, by the cycloid scales,

Fig. 879.—*Lepidosiren paradoxa*, from South America. Reduced.
p, Pectoral; *v*, Pelvic fin.

the absence of jugular plates, the continuous vertical fin, and the narrow central axis of the paired fins, which are reduced to filaments. The two genera are *Lepidosiren* (fig. 879) of the Amazons, in which the paired fins are not fringed; and *Protopterus* of the rivers of tropical Africa, where those fins are furnished with fringes. There

Fig. 880.—The Barramunda (*Ceratodus Forsteri*), from Queensland. Reduced.

are two small conical vomerine teeth, and larger cuspidate teeth on the palate, while the body is eel-like.

Family Ceratodontidæ.—The genus *Ceratodus* (fig. 880) has been generally placed in the same family as the preceding forms, with which it agrees in the continuous vertical fin, the cycloid scales, the absence of jugular plates, and the few cranial bones. In many

respects, and more especially as regards the dentition, *Ceratodus*, as pointed out by Dr Fritsch, is, however, much more nearly allied to the under-mentioned family *Dipteridæ*, and it seems advisable to regard it as representing, at least provisionally, the type of a distinct family.

Ceratodus is one of the very few instances where a genus, founded upon the evidence of fossil specimens, has subsequently been discovered in a living condition. Fossil teeth of this genus were long known, but it was not until the year 1870 that the existence of a living representative was brought to the notice of science. The body of the Barramundas, as these fishes are termed, is laterally compressed, with one continuous vertical fin; while the paired fins are paddle-shaped, with a broad fringe. The vomerine teeth (fig. 881, x) are shaped like the incisors of many mammals, while those on the palate (*ibid.*, xx) and mandible have an inner smooth convex border, and externally bear a number of strongly-marked ridges or horns. In the existing species the teeth of opposite sides are separated by a distinct interval (fig. 881), but in some fossil forms they were in contact. Again, in the living species, the palatal teeth bear six distinct horns, while the backward production of the inner margin forms an incomplete seventh horn (fig. 881); but in the mandibular teeth there are not more than the typical six horns. In fossil forms, according to Professor Miall, the mandibular teeth are slightly smaller and narrower than the palatal ones, and have not more than four horns; while the palatal teeth have either five horns, or four and a rudiment of a fifth (fig. 882); this simpler structure of the teeth in the earlier forms being analogous to that which we have already mentioned as obtaining in the Selachian *Notidanus*. Some of the fossil teeth indicate individuals of two or three times the size of the Barramunda, of which the largest specimens attain a length of nearly six feet. The position of these upper teeth on the palatopterygoid bar is well shown in fig. 881, which also ex-

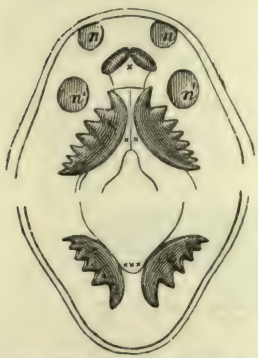

Fig. 881.—Mouth of *Ceratodus Forsteri*. Reduced. x, Vomerine; xx, Palatal; xxx, Mandibular teeth; *n*, anterior; *n'*, Posterior nares.

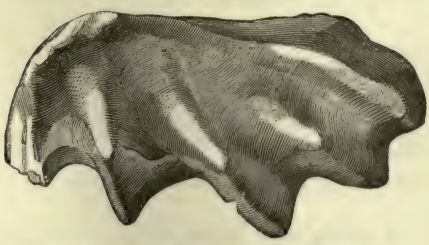

Fig. 882.—The right palatal tooth of *Ceratodus Hislopianus*, from the Lower Gondwanas of Maleri, India. The left side is the anterior border.

hibits the large parasphenoid, and the anterior and posterior nares. In regard to its distribution in past times, we meet with remains of this genus in the Jurassic of Colorado and Montana in the United States, and also in the Lower Jurassic of Stonesfield near Oxford; it is, moreover, abundant in the Upper (Keuper) and Middle (Muschelkalk) Trias of Europe, and has been recorded from the Lower division (Bunter) of that formation; it also occurs in Illinois in beds, which are thought to be probably Triassic; while in India teeth are very common in the Maleri group of the Gondwana system of the Central Provinces, which is not improbably also of Triassic age. Further, Professor Cope has recorded the genus from strata in North America identified by him with the Permian; but the species from the European Permian originally referred to this genus belongs to *Ctenodus*.

Family Phaneropleuridæ.—In this family, which has been placed by some in the Crossopterygian Ganoids, we still have the

Fig. 883.—*Phaneropleuron Andersoni;* from the Devonian of Scotland, one-half natural size. A, Scale magnified.

continuous vertical fin, the diphycercal caudal fin, and the narrow axis of the paired fins characteristic of the preceding families; but the scales are said to have a ganoidal structure, jugular plates are present, and there is a series of minute teeth in the margins of the jaws. This family is typically represented by *Phaneropleuron* (fig. 883), of the Devonian and Carboniferous of Scotland and the Devonian of Canada, and the allied *Uronemus* of the Scottish Carboniferous. We may, however, here mention the genera *Megapleuron*[1] and *Conchopoma* from the Permian of the Continent, which should probably find a place in this or an allied family. The former genus has

[1] The rhomboidal scales which have been described as belonging to this genus are those of a Ganoid. The name should properly be *Megalopleurum*.

ossified ribs, large operculars, and Dipnoid teeth, but the form of the fins and tail is unknown; while the latter agrees with *Phaneropleuron* in the structure of the teeth and tail.

Family Dipteridæ.—This family is characterised by the great development of the cranial bones, the more or less ganoidal structure of the scales, the presence of jugular plates, the heterocercal tail, the two distinct dorsal fins, and the greater size and breadth of the scaled portion of the paired fins. Its range extends from the Devonian to the Permian, and it shows signs of connecting the preceding family with the Crossopterygian Ganoids. The teeth (fig. 885) are of the same general type as those of *Ceratodus*, but may carry a larger number of smaller ridges, which in some instances (fig. 885, 1, 2) are ornamented with a number of cusps or denticules. The typical genus *Dipterus* (fig. 884) comprises fishes of small or medium size, with circular scales, and both the dorsal fins placed in the hinder third of the body, the first being much smaller than the second. The pectoral fins are long and paddle-

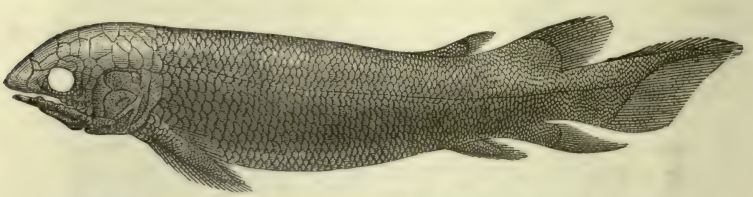

Fig. 884.—*Dipterus Valenciennesi*; from the Devonian of Russia, two-thirds natural size. (After Pander.)

shaped; while the pelvic pair, and the anal, are respectively placed beneath the first and second dorsals. The quadrate is ossified; and there are also ossifications in the fin-rays and ribs. The teeth (fig. 885, 1) carry numerous denticules on their ridges. This genus is characteristic of the Devonian (Old Red Sandstone) of Europe. *Ctenodus* attains considerably larger dimensions than the preceding genera; some of the species reaching a length of nearly five feet. The teeth are characterised by their ridges carrying many cusps; and the scales are large and thin, with a rhomboidal contour, and bearing traces of rows of denticules, with vascular grooves on the inner side. The skeleton closely resembles that of *Ceratodus*, but is more fully ossified; and both this feature and the more numerous cranial bones are regarded by Dr Fritsch as characters of greater specialisation. The teeth (fig. 885, 2, 3) are frequently simpler than those of *Dipterus*, and thus approximate to those of *Ceratodus*; while the form of the parasphenoid and palatopterygoid differs considerably from that in the former. This genus ranges in Europe from the Carboniferous to the Permian, being very abundant in the

former; and it is also recorded from strata in Illinois and Texas which are correlated with the European Permian.

As members of this order, but perhaps indicating one or more distinct familes, we may class the following genera: *Palædaphus*, from the Devonian of Europe and Ohio (the species from the latter area having been separated as *Heliodus*), is a moderately large form in which the mandibular teeth (fig. 885, 4) are very broad, and carry

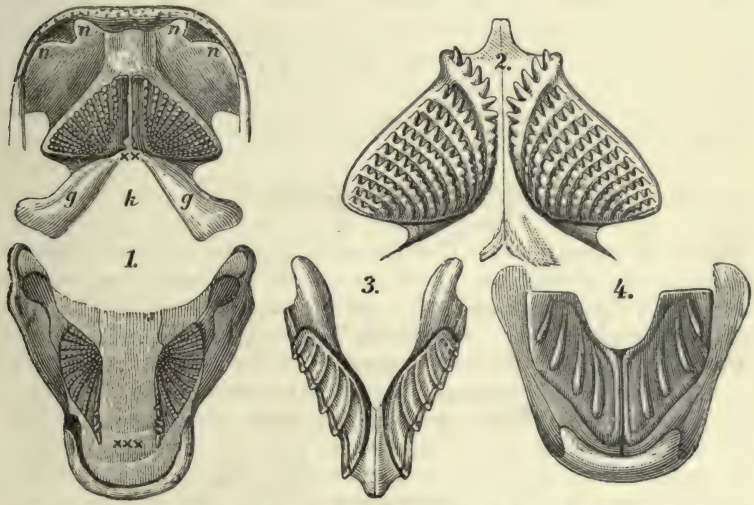

Fig. 885.—1, Upper and lower jaws of *Dipterus Valenciennesi;* from the Devonian. xx, Palatal; xxx, Mandibular teeth; *n*, *n*, Narial processes; *g*, Palatopterygoid. 2, Palate of *Ctenodus tuberculatus;* Carboniferous. 3, Mandible of *Ctenodus imbricatus;* Carboniferous. 4, Mandible of *Palædaphus insignis;* Devonian. All reduced.

only four low ridges. *Holodus*, from the Devonian of Russia, is a smaller form very imperfectly known, but apparently allied to the preceding; while *Conchodus* is known by teeth from the same deposits in both Scotland and Russia. *Ganorhynchus*, of which the horizon is unknown, may also be provisionally placed here. From North America we have *Ptyonodus* and *Gnathorhiza* from the Permian, and *Mylostoma* from the Devonian, of which the full affinities require further elucidation.

CHAPTER XLIX.

CLASS PISCES—continued.

Order Ganoidei.

Order V. Ganoidei.—The Ganoids form an order exceedingly difficult of definition, owing to their close connection on the one hand with the Dipnoi and (through the Acanthodea) the Elasmobranchei, and on the other with the Teleostei, and it is not improbable that it may be eventually necessary to divide them into at least two orders. As mentioned above, some writers group them in a subclass with the Teleostei under the name of Teleotomi. The body may be either naked or covered with shagreen skin, or with large detached bony scales, or completely covered either with true ganoid scales, or with cycloidal scales of a ganoid structure. The vertebral column, again, may be either cartilaginous or fully ossified; and its termination in the tail may be either diphycercal or heterocercal. Paired and median fins are generally present, and the pelvic pair (with perhaps one exception) is abdominal in position. The skull may either be covered merely by cranial membrane bones, or may be completely ossified. It is hyostylic—*i.e.*, there is a hyomandibular suspensorium—and the palatopterygoid is distinct from the cranium; and, as a general rule, even in the cartilaginous forms maxillæ and dentary bones, which carry the teeth, are developed on the palatopterygoid and Meckel's cartilage respectively. The gills are usually free, and their single aperture is covered by an operculum; while branchiostegal rays are very generally present. In most cases a secondary pectoral girdle of dermal bones (clavicular, supraclavicular, &c.) is developed externally to the cartilaginous scapulo-coracoidal girdle, which alone exists in the preceding orders. Finally, there is a swim-bladder, with a duct into the pharynx; while there are some other characters of the soft parts into the consideration of which it will not be necessary to enter in this work.

Some very curious features occur in the ossification of the ver-

tebral column of certain members of this order which call for passing notice. Thus in *Eurycormus* the ossifications in the dorsal region consist of an upper and a lower hollow, wedge-shaped, semi-cylinder, with their pointed extremities interlocking, and the former bearing the neural arches and the latter the ribs; while in the tail we have two centra to each neural arch. From this it would appear that the pieces bearing the ribs in the dorsal region, and the caudal centra which have no arches, correspond to the intercentra of the Amphibia, which are noticed below. The teeth of Ganoids vary greatly in structure, and may be either conical and borne on the margins of the jaws, when they are continuously replaced, or flattened disks attached to the vomer, which have no successors. The borders of the fins are frequently furnished with the modified scales known as fulcra.

Considerable diversity of view has prevailed as to the classification of Ganoids; but the system of Dr Traquair, who has paid especial attention to the structure of the order, is adopted in this work.

As regards their distribution in time, Ganoids first appear in the Silurian nearly at the same time as the Elasmobranchs; and from the Devonian to the close of the Mesozoic they form a very large proportion of the Fish-life of those periods. Their wane, however, appears to have set in during the Upper Cretaceous, when the Teleostei began to be numerically strong; and from that date there has been a rapid decrease to the present day, when we find only one of the suborders (Amioidea) represented by several genera; while of the other three surviving suborders one is represented by two genera, and each of the other two by a single genus—these four genera each having a solitary species.

A. Proganoid Series.—The first three suborders may be conveniently grouped in a single series, and are mainly characterised by their exceedingly low development, their affinities being still doubtful. Professor Cope is indeed disposed to regard one of these suborders (Placodermata) as more nearly allied to the Tunicata than to other Vertebrata; but this view is scarcely likely to find acceptation with the majority of palæontologists.

Suborder 1. Cephalaspidea.—The members of this extraordinary group have the head and the anterior part of the body covered with a continuous shield, while the rest of the body is coated with small angular plates or scales. No traces of an inner skeleton, lower jaw, or teeth, have yet been discovered; but at least in the second family there was a strong pectoral fin at the hinder extremity of the dorsal shield. The latter has been recently shown to be furnished with a system of sensory canals. This group is confined to the Silurian and Devonian; and it is suggested by Professor Huxley that it may be allied to the Acipenseroidea.

Family Pteraspididæ.—The entire body in this family is unknown; but the dorsal shield (figs. 886, 887) is usually composed of several pieces united together, and has its borders thickened and

Fig. 886. — Imperfect dorsal shield of *Cyathaspis Banksi*; from the Silurian of Ludlow. (After Murchison.)

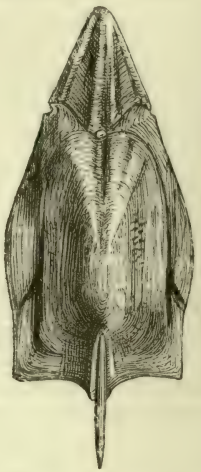

Fig. 887. — Dorsal shield of *Pteraspis rostrata*; from the Lower Devonian of Hereford. Reduced. (After Lankester.)

bent, and in structure approaches the scales of Teleostean Fishes. It has a median posterior spine, and sometimes small lateral cornua. There is also a small shield on the ventral aspect of the fish, which, like the dorsal one, is marked by fine striations. In the type genus *Pteraspis*, the dorsal shield (fig. 887) is shaped like an arrow-head, and composed of seven pieces; while in *Cyathaspis* (fig. 886) it is oval, composed of only four elements, and has the posterior spine very short. *Scaphaspis* has been founded on

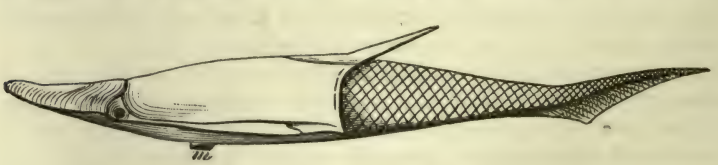

Fig. 888.—Reduced restoration of *Pteraspis*.

remains belonging to these two genera, which are found in both the Silurian and Devonian; the simple shields described under this name having apparently been placed ventrally beneath the more complex ones, on the evidence of which the other genera were

founded. *Holaspis*, from the Lower Devonian of North Wales, is distinguished by the dorsal shield, consisting of only a single element. Figure 888 is an attempt to restore the form of the type genus.

Family Cephalaspididæ.—The Cephalaspids are regarded by some writers as belonging to the *Pteraspididæ*, while by Professor Zittel they are placed in a distinct suborder. The dorsal cephalic shield (fig. 889) consists of one or two pieces, and usually has more or less developed lateral cornua, with a regularly curved and flat lower border—the eyes being situated near the middle; in structure it resembles true bone. The body is covered with bony plates, and the caudal fin is heterocercal. The typical genus *Cephalaspis* (figs.

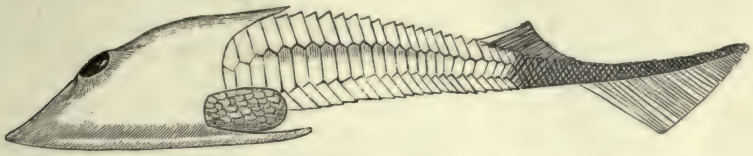

Fig. 889.—Left lateral view of *Cephalaspis Lyelli*; from the Devonian of Scotland. About one-third natural size. (After Lankester.)

889, 890) has the cephalic shield single, and may be divided into the *Eucephalaspidine* and *Hemicephalaspidine* groups, according to the degree of development of the cornua. It occurs in the Silurian and the Devonian of Britain, and has also been obtained

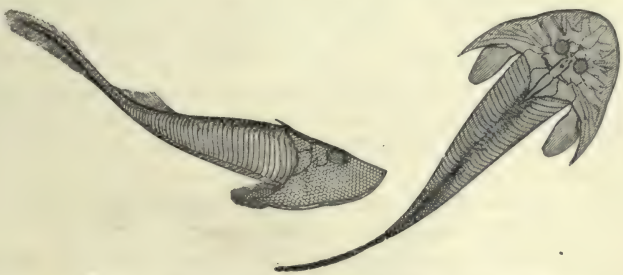

Fig. 890.—Smaller views of *Cephalaspis Lyelli*. (After Page.)

from the Silurian of Bohemia and the Devonian of Canada. *Xenaspis*, from the same English formations, is distinguished by the presence of one or more quadrangular dorsal plates behind the head; while *Auchenaspis*, of the European Silurian, has the cephalic shield transversely divided. *Didymaspis*, from the same formation, agrees with the latter in its double cephalic shield, which is, how-

ever, unprovided with cornua; while other genera are *Thyestes* and *Trematapsis*, from the Silurian of Russia.

Suborder 2. Placodermata.—This suborder is mainly characteristic of the Devonian, although represented also in the Silurian, and lingering on till the Permian. It is characterised by the cartilaginous vertebral column, and the enclosure of the head and the anterior part of the body in bony plates, which are covered with a radiate or granular sculpture; the tail being either naked or clothed with scales. There is a distinct mandible; teeth are frequently present; and there may be a jointed pectoral fin enclosed in a bony covering like that of the body, but pelvic fins are invariably absent.

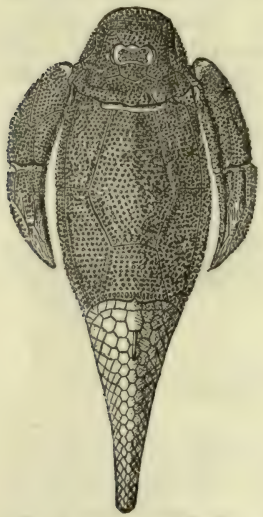

Fig. 891.—Reduced restoration of the dorsal aspect of *Asterolepis ornata*; from the Devonian of Russia. The tail is restored from *Pterichthys*. (After Pander.)

Family Asterolepididæ.—In the typical family the head (figs. 891, 892) is rounded anteriorly, and covered with a number of small thin plates; while the body is sub-quadrangular and invested with larger plates, some of which are median and others paired; and the tail may either be covered with much smaller scales or naked. There is a well-developed pectoral limb, which articulates with the anterior ventro-lateral plate; although it was long thought to articulate in some forms to a separate thoracic plate. The type genus *Asterolepis*, which occurs both in Russia and Scotland, is characterised, according to Dr Traquair, by the anterior median dorsal plate overlapping both the anterior and the posterior dorso-laterals, and by the somewhat depressed body. In *Pterichthys* (figs. 892, 893), on the other hand, the median dorsal plate, while overlapping the anterior dorso-laterals, is itself overlapped by the posterior dorso-laterals, and the body is much more elevated. This genus has been recorded from Scotland and the Eifel, and probably also occurs in Russia. Detached pectoral fins of these genera have been described under several names, and were at one time regarded as ichthyodorulites.

The genus *Bothriolepis*, from the Devonian of Europe and Canada, is distinguished by the different contour of the cephalic plates, and of the grooves of the lateral line system by which they are marked, as well as by the shorter limbs. No traces of the scaly tail have been observed in any of the known specimens, although

Dr Traquair considers that this appendage was probably present. Some of the species attained very large dimensions.

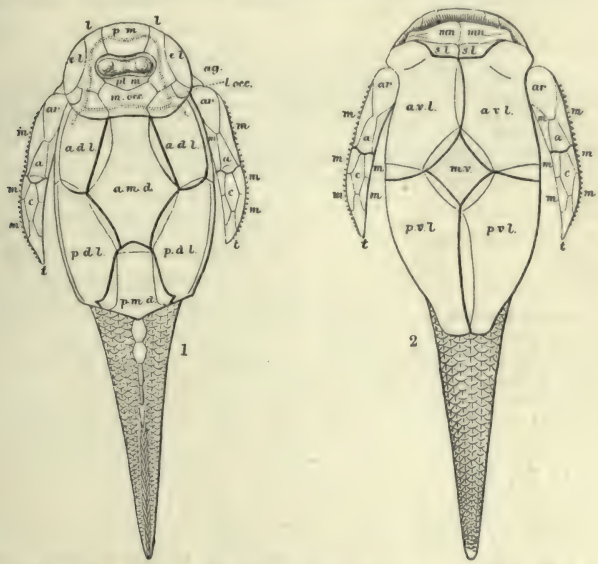

Fig. 892.—Reduced restoration of the dorsal (1) and ventral (2) aspects of *Pterichthys cornutus*, with the sculpture omitted; from the Devonian of Scotland. The thin black lines indicate the concealed edges of the overlapped plates, and the double dotted lines the grooves of the lateral line system. *m.occ*, Median occipital plate; *l.occ*, Lateral do.; *ag*, Angular plate; *pt.m*, Postmedian do.; *p.m*, Premedian do.; *l*, Lateral do.; *e.l*, Extra-lateral do.; *mn*, Mental do.; *s.l*, Semilunar do.; *a.m.d*, Anterior median dorsal do.; *p.m.d*, Posterior do. do.; *a.d.l*, Anterior dorso-lateral do.; *p.d.l*, Posterior do. do.; *a.v.l*, Anterior ventro-lateral do.; *p.v.l*, Posterior do. do.; *m.v*, Median ventral do.; *ar*, Articular plate of limb; *a*, Anconcal of do.; *c*, Central of do.; *m*, Marginal of do. (After Traquair.)

Microbrachius, of the Scottish Devonian, is an allied form distinguished by the smaller size of the pectoral limb; in this form also

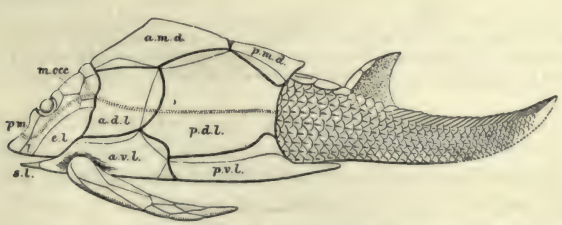

Fig. 893.—Reduced left lateral aspect of *Pterichthys cornutus*; from the Devonian of Scotland. Letters as in the preceding figure. (After Traquair.)

no caudal scales have been observed. The length of the head and carapace in the one known species is one and a quarter inches.

Family Coccosteidæ.—The genus *Coccosteus* differs so markedly from the members of the preceding family that Dr Traquair has suggested that it should form the type of a distinct suborder. The head has distinct bones and plates differing markedly in their arrangement from those of the preceding family, but their structure has only recently been rightly explained (fig. 894). In the restoration given by Agassiz (fig. 895), although the arrangement of the posterior plates is fairly correct, yet anteriorly the grooves of the lateral line were mistaken for sutures; while the ethmoidal bones at the muzzle and the orbital notches are omitted. An approximation to a correct restoration of the lateral aspect is shown in fig. 896, but the mouth is made too long. The carapace, or body-shield, consists of a long shield-shaped middle dorsal plate, flanked by lateral plates, and completed by a median ventral plate. The posterior half of the body is totally unprotected, but interspinous bones in the vertebral column support an anal and a

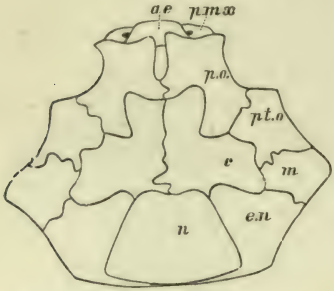

Fig. 894.—Dorsal aspect of the cranium of *Coccosteus decipiens*; from the Devonian of Scotland. *ae*, Ethmoidal, with nares of either side; *p.m.x*, Premaxilla; *p.o*, Preorbital, external to which is the orbit; *pt.o*, Postorbital; *c*, Central, *m*, Marginal, *n*, Middle occipital; *e.n*, Lateral do. (After Traquair.)

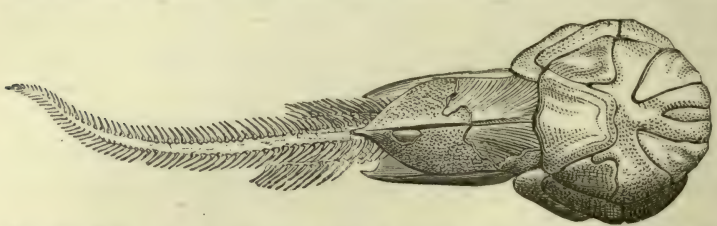

Fig. 895.—Dorsal view of *Coccosteus decipiens*, as restored by Agassiz. In the anterior part of the head the ethmoids and orbits have been omitted, and the black lines mostly indicate the grooves of the lateral line system, and not sutures. The shield-shaped plate immediately behind the skull is the middle dorsal, in advance of which is the middle occipital of the skull.

dorsal fin. There appears to have been no pectoral fin, although certain forms which have been generically or subgenerically separated as *Brachydirus* have been represented with such an appendage. Both this and the next genus are characteristic of the Devonian, *Coccosteus* being common to Europe and Canada. The allied *Homosteus* includes gigantic forms from Scotland and the Eifel, readily distinguished by the form of the cranial and body plates. Thus the middle occipital plate is longer and narrower, and the middle dorsal wider than long, and not pointed behind. Professor Huxley

compares the armour of the Coccosteans to that of the Siluroid Teleosteans; while Newberry and Pander compare the ventral armour with the plastron of the Chelonia and Labyrinthodontia, with

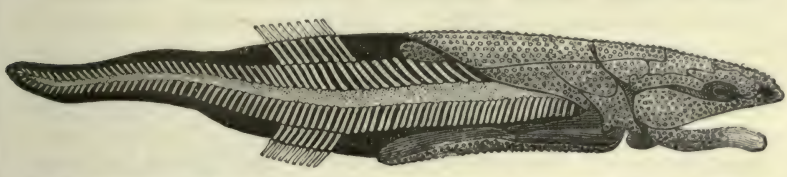

Fig. 896.—Approximate restoration of the right lateral aspect of *Coccosteus decipiens*. Here the ethmoids and orbits are introduced, but the skull and mouth are made too long.

which, however, they also compare the true pectoral girdle of the Sauropterygia. The nature of the dentition is unknown.

Family Dinichthyidæ.—The genus *Dinichthys*, from the Devonian (Huronian) of North America, may probably be regarded as forming the type of a family allied to the preceding. In this genus, of which the type species has an estimated length of from 15 to 18 feet, the dentition (fig. 897) is remarkably like that of the Dipnoid

Fig. 897.—Diagrammatic anterior aspect of the jaws of *Dinichthys Hertzeri*; from the Devonian of North America. One-twelfth natural size. (After Newberry.)

genus *Protopterus*, from which Dr Traquair concludes that there was probably a close connection between the present group and the Dipnoi. Other gigantic forms more and less closely allied to the type genus are *Titanichthys*, *Liognathus*, and *Diplognathus*, from the Devonian of Ohio; while *Typodus*, from the same formation in the Eifel, may perhaps belong to this family.

As Placodermata, of which the serial position is uncertain, may be mentioned *Menaspis*, from the Permian of Germany; *Acanthaspis*, *Acantholepis*, and *Aspidichthys*, from the Devonian of Ohio; *Pnigeacanthus* and *Lecracanthus*, from the Carboniferous of Iowa; *Stichacanthus* and *Phoderacanthus*, from the corresponding formation of Ireland and Belgium; and *Anomalichthys*, from the Devonian of Germany.

Suborder 3. Acanthodea.—The last group of the Proganoids is also Palæozoic, and ranges from the Devonian to the Permian, although it is not improbable that some of the genera, founded upon fin-spines, which are noticed under the Elasmobranchei, should be

placed in it. The Acanthodeans appear to be in some respects intermediate between the Ganoids and Elasmobranchs, and should perhaps constitute an order by themselves. They have the body, which is more or less elongated and compressed, covered with shagreen-like scales, and with the lateral line running between two rows of such scales. The tail is heterocercal; and the fins have strong spines, which, except in the pectorals, are merely inserted between the muscles. There is considerable doubt as to the presence of cranial bones or of a gill-cover; but there is a ring of bones round the orbit. The vertebral column is cartilaginous, and teeth are either wanting or are very minute and sharp.

In their cartilaginous skeleton, the not improbable absence of an operculum, the structure of the scales and position of the lateral line, as well as in the spines of the median fins, the Acanthodea approach the Elasmobranchei; but the articulation of the pectoral fin-spine to the pectoral girdle is a character of the Teleostean *Siluridæ*, while the orbital ring is a character of the higher Ganoids like the *Palæoniscidæ*.

Family Acanthodidæ.—All the genera may be provisionally

Fig. 898.—*Acanthodes;* from the Permian of Europe. (After Kner and Roemer.)

included in a single family, of which the type genus *Acanthodes* (fig. 898), as now restricted, ranges from the Carboniferous to the Permian of Britain and the Continent. The head is very short and blunt, and there is but a single dorsal fin placed immediately above the anal, while it is thought that teeth were absent. *Mesacanthus*, of the Scottish Devonian, includes small fishes distinguished from the last genus by the presence of an intermediate pair of small spines between the pectoral and pelvic fins; it is represented in the Devonian of Canada. Closely allied is *Acanthodopsis*, from the Carboniferous of Northumberland, in which there were numerous minute teeth; while *Chiracanthus* (fig. 899, 1), of the Scottish Devonian, is distinguished by the dorsal fin being placed in advance of the anal. In *Diplacanthus* (fig. 900) there are two dorsal fins, of which the second is placed above the anal; each pectoral fin has two spines; while there are minute spines between the pectoral

and pelvic fins, and the jaws are furnished with small conical teeth. This genus is represented by several species in the Devonian of Scotland, and not improbably also occurs in that of Canada. *Rhadinacanthus*, from the Scottish Carboniferous,

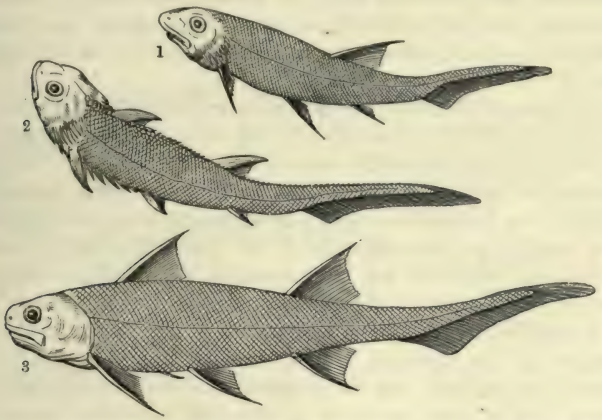

Fig. 899.—1, *Chiracanthus Murchisoni*; 2, *Climatius scutiger*; 3, *Ischnacanthus gracilis*; from the Devonian of Scotland. Reduced.

has two in place of four pectoral spines; while in *Ischnacanthus* (fig. 899, 3), of the same deposits, the small intermediate spines are wanting, although they are introduced in the figure. Allied to the last are *Euthacanthus* and *Parexus*, from the Scottish Devonian, the former having the second dorsal in advance of the anal

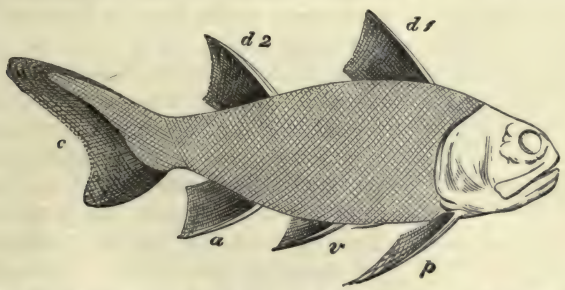

Fig. 900.—*Diplacanthus striatus*; from the Devonian of Scotland. *p*, Pectoral; *v*, Pelvic; *a*, Anal; *c*, Caudal; d^1, d^2, First and second dorsal fins. Reduced.

fin. Finally, the genus *Climatius* (fig. 899, 2) includes three small fishes from the last-named formation characterised by the short fin-spines and the presence of a series of accessory spines between the pectoral and pelvic fins. There are two dorsal fins, of which the

second is behind the anal, the figure being incorrect in the latter respect. Fin-spines from the Devonian of Canada, described as *Ctenacanthus* and *Homacanthus*, are referred by Mr Woodward to *Climatius*.

Incertæ Sedis.—Here may be noticed the family *Tarrasiidæ*, proposed by Dr Traquair for the imperfectly known genus *Tarrasius*, from the Scottish Carboniferous, which is regarded as indicating an aberrant type.

B. Euganoid Series.—The remaining members of the order include its typical representatives, and may be collectively known as the Euganoid series or the Ganoidei Veri.

Suborder 4. Crossopterygea.—In this group the pectoral, and sometimes the pelvic, fins consist of a central lobe surrounded by a fringe; there is an infraclavicular in the pectoral girdle; the rays of the dorsal and anal fins are often more numerous than the supporting interspinous bones; the preopercular extends forwards on the cheek; branchiostegal rays are replaced by jugular plates; the development of the vertebral column varies; the tail may be either diphy- or heterocercal, and the scales cycloidal or rhomboidal. This suborder is the most primitive of the true Ganoids, among which it holds a position somewhat analogous to that occupied by the Ichthyotomi in the Elasmobranchei.

Family Holoptychiidæ.—In the type family the pectoral fins are acutely, and the pelvic subacutely, lobate; the skeleton of the former, according to Dr Traquair, being a biserial archipterygium like that of *Ceratodus*. The teeth are of the so-called *dendrodont* type, the dentine of the base being infolded in an extremely complex manner, with cross-branchings which form an intricate network within the crown. The scales are cycloidal, thick, and sculptured; and there are two dorsal fins, and a heterocercal tail in which the inferior rays are much longer than the superior. Before noticing the typical forms we may briefly mention the genus *Onychodus*, from the Devonian of North America and Europe, which Dr Newberry considers may be allied to this family. The scales (fig. 901) have distinct ridges, and the mandible has a presymphysial production furnished with teeth arranged somewhat like an old-fashioned cavalry spur. The type genus *Holoptychius* (fig. 902) comprises fishes, which are often of large size, from the Devonian of Europe and North America. The two dorsal fins are placed in the hinder part of the body directly over the pelvic and anal. We may probably place here the imperfectly known

Fig. 901.—Scale of *Onychodus sigmoides*; from the Devonian of North America. (After Newberry.)

Platygnathus, from the Devonian of Scotland and Russia; *Isodus*, of the Irish Carboniferous; and *Peplorhina*, from the Trias of Illinois. In *Glyptolepis* (fig. 903), from the European and Canadian Devonian, we have a well-known form in which the dorsal fins are placed more anteriorly than in *Holoptychius*, while the anal is situated below the first dorsal, and the pelvic are consequently much

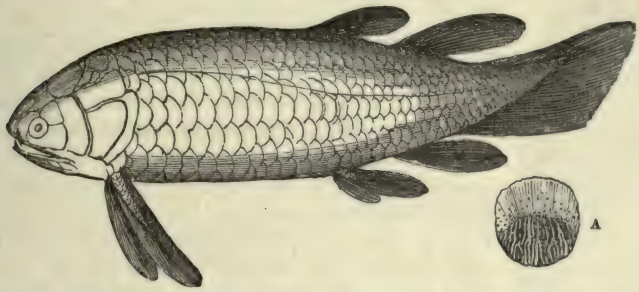

Fig. 902.—*Holoptychius nobilissimus*; from the Devonian of Scotland. A, A scale less reduced. The dorsal and anal fins should be more pointed.

more approximated to the pectoral fins. *Phyllolepis*, founded on very thick scales, which are sometimes smooth, from the Devonian and Carboniferous of Scotland, should probably be included in this family, in which Dr Traquair also places the imperfectly known genus *Dendrodus*, of the Devonian of Russia and Scotland. The jaws of the latter carry a small row of marginal teeth of conical form; while in the mandible there is a second row of much larger fang-like teeth, each of which has a distinct socket. These teeth

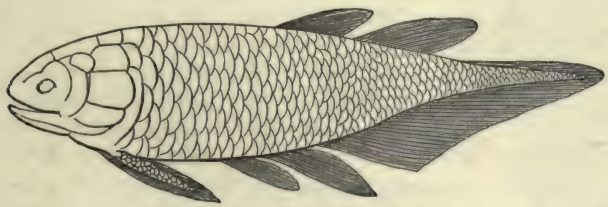

Fig. 903.—Restoration of *Glyptolepis*; from the Devonian of Scotland. Reduced. (After Huxley.)

are somewhat compressed, with trenchant fore-and-aft edges, and have the internal structure already noticed. *Colonodus*, of the British Carboniferous, and *Sigmodus*, of the Upper Palæozoic of northern India, should perhaps find a place in this family.

Family Rhizodontidæ.—In the Rhizodonts the pectoral fins are subacutely or obtusely lobate, the pelvic pair being usually non-

lobate; while their internal skeleton forms a shortened uniserial archipterygium. The teeth are labyrinthodont in structure, lacking the complex internal network found in the preceding family. The scales are cycloidal and sculptured; the median fins are numerically the same as in *Holoptychius;* but the tail approximates to the truly diphycercal type. The lower jaw has an inner series of tusk-like teeth (fig. 905). As an imperfectly known form we may first mention *Cricodus* (*Polyplocodus*) from the European Devonian. In the well-known *Tristichopterus*, of the Scottish Devonian, the body is much elongated, the tail distinctly heterocercal, the posterior fins are placed near the tail, the opercular bones are unusually large, and the scales thin and striated. An apparently allied form is *Eusthenopteron* of the Devonian of Canada, in which the vertebral centra appear to have been unossified, while there are slight differences in the interspinous bones, tail, and teeth. According to the views of Dr Traquair, *Gyroptychius* (fig. 904), from the Devonian of Scotland, is allied to *Tristichopterus*, having scales of the same general type (although some of these were formerly thought to be rhomboidal), but a more rhomboidal tail, and the exposed portion of the scales relatively larger. From the Carboniferous of both Europe and North America we have the type genus *Rhizodus* (*Megalichthys* in part), of which the typical species attained a very large size. The larger teeth (fig. 905), on the evidence of which the genus was originally founded, have the upper half of the crown smooth, while the lower half is longitudinally fluted. The teeth of large individuals (which may attain a length of nine feet) are nearly two inches in height. In *Rhizodopsis*, of the same deposits, the cranial bones form a well-developed shield on the superior surface resembling that of the *Osteolepididæ*, although the mandible agrees in general structure with that of *Rhizodus*, and consists of articular, angular, and dentary elements; the latter having a series of *infra-dentary* pieces on its inner side which carry the large tusk-like teeth. The inferior space between the mandibular rami is occupied by a series of jugular plates, of which there is a large median pair, together with a small unpaired anterior

Fig. 904.—*Gyroptychius angustus;* from the Devonian of Scotland. Reduced. (After Pander.)

one, and a row of small lateral ones on either side. In the cranium the most striking feature is the anterior position of the orbit, which has three large suborbital bones behind it. Other more imperfectly

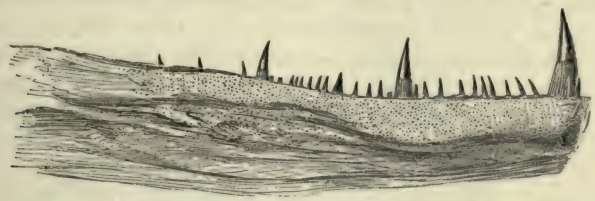

Fig. 905.—A mandibular ramus of *Rhizodus Heberti*; from the Carboniferous of Scotland. Reduced.

known genera of this family from the European Carboniferous are *Dendroptychius*, *Strepsodus*, *Rhomboptychius*, and *Archichthys*.

Family Osteolepididæ (Rhombodipteridæ).—In this family the fins have the same general structure as in the preceding; but the scales are of the rhomboidal form typical of the order. There are a number of lateral jugular plates; the teeth are numerous and sharply-pointed; and the ossification of the vertebral column is

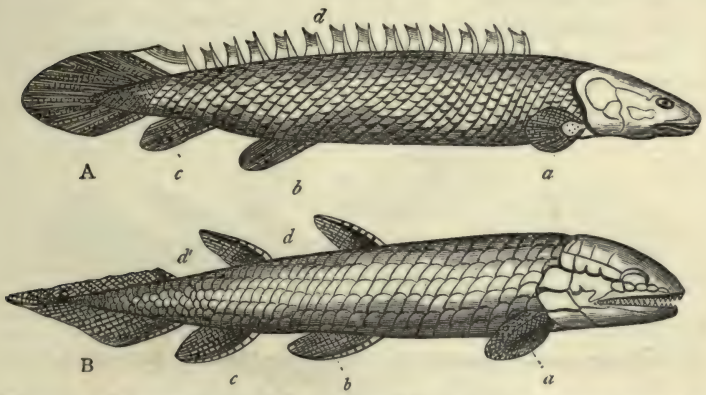

Fig. 906.—A, *Polypterus bichir*; from the Upper Nile. B, *Osteolepis macrolepidotus*; from the Devonian of Russia. (After Pander.) Both figures reduced. *a*, Pectoral; *b*, Pelvic; *c*, Anal; *d*, *d'*, Dorsal fins. In the lower figure the dorsal fins should be placed more in advance of the pelvic and anal.

imperfect. The family is divided into two subfamilies; the first, *Osteolepidinæ* (*Saurodipterini*) being characterised by the smooth scales, and presence of a median jugular plate. The type genus *Osteolepis* (fig. 906, B) has a long and slender body, with the two dorsals placed respectively in advance of the pelvic and anal fins. The type species is of considerable size. In the allied *Thursius*, of

which an immature individual is shown in fig. 907, the dorsals are placed immediately over the pelvic and anal fins. Both genera occur in the Devonian of Scotland and Russia. Closely allied is the genus *Diplopterus*, from the Scottish Carboniferous, in which the dorsal fins are also situated posteriorly, the first being directly over the pelvic. *Megalichthys*, from the same deposits, comprises two species of large size; and is characterised by the presence of large fulcra at the roots of the pectoral, pelvic, and anal fins; and also by the

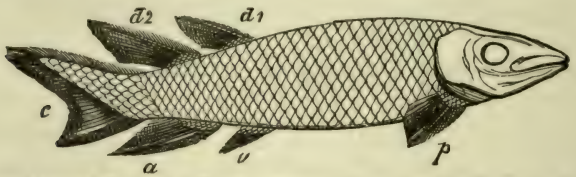

Fig. 907.—A young individual of *Thursius macrolepidotus*; from the Devonian of Scotland. Letters as in fig. 900. Reduced. (After Sedgwick and Murchison.)

small size of the anterior dorsal fin, which is placed above the pelvic fin. *Ectosteorhachis*, from the Permian of North America, is nearly related, and appears to be the last survivor of the family. The second subfamily, or *Glyptolæminæ*, is represented only by the genera *Glyptolæmus* (fig. 908) and *Glyptopomus*, of the Scottish Devonian; and differs from the last by the sculptured scales, and the absence of a middle jugular plate. The body is much elongated; there is a long interval between the pectoral and the posterior

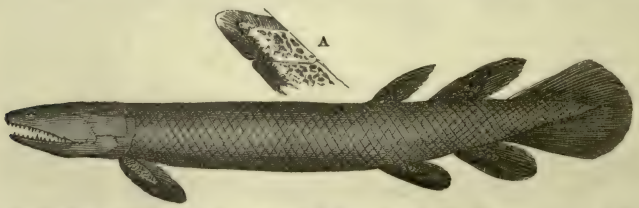

Fig. 908.—*Glyptolæmus Kinnairdi*; from the Devonian of Scotland. Reduced. A, Scales. (After Huxley.)

fins; and the tail is truly diphycercal; each genus is represented by a single species.

Family Cœlacanthidæ.—With this family we come upon a group of fishes not occurring in the older Palæozoic, but extending from the Carboniferous to the Upper Cretaceous, and thus affording a link between the preceding extinct and the following existing family. The vertebral column is unossified; there are two dorsal fins, each of which is supported by a single forked interspinous bone; the pectoral fins are obtusely lobate; the caudal fin is un-

usually large, and completely diphycercal; the swim-bladder is ossified, and the scales are cycloidal. The members of this family are further characterised by the full development of the cranial bones; and the arrangement of the ossifications in the orbit ap-

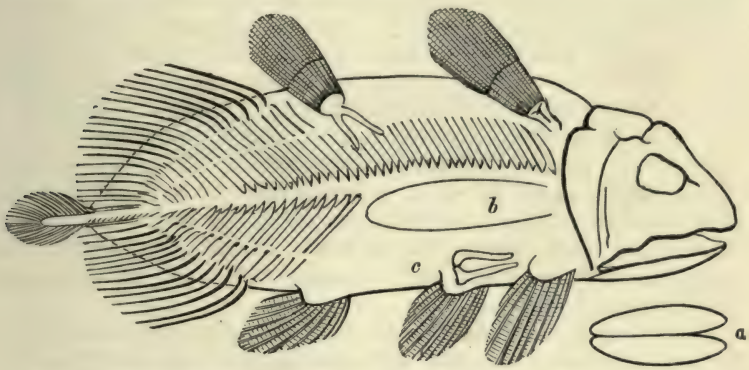

Fig. 909.—Skeleton of *Undina penicillata*; from the Kimeridgian of Bavaria, one-fourth natural size. *a*, Jugular plates; *b*, Swim-bladder; *c*, Pelvis.

proaches that found in the Labyrinthodontia. The type genus *Cœlacanthus* ranges from the Carboniferous of Europe and North America to the Upper Trias of the former area, and is well characterised by the great thickness of its scales.

More or less nearly allied are *Diplurus* from the Trias of New

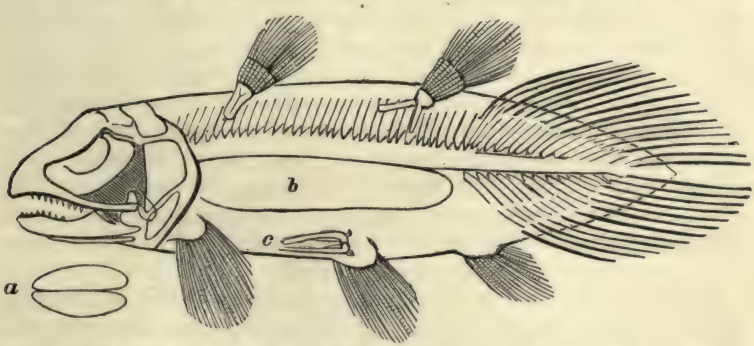

Fig. 910.—Skeleton of *Macropoma Mantelli*; from the Chalk of Sussex. Reduced. Letters as in fig. 909. (After Huxley.)

Jersey, *Graphiurus* from the Upper Trias of Carniola, and *Heptanema* ranging from the Middle Trias to the Upper Jurassic of the Continent. In *Undina* (fig. 909) the exposed parts of the scales are marked by ridges, rising in some parts into spines, and the

rays of the dorsal and caudal fins are divided and furnished with spines. In the English Liassic *Holophagus* the spines on the scales are more numerous, while in *Libys*, from the Kimeridgian of Bavaria, they are less numerous, the division of the fin-rays extends more deeply than in *Undina*, and the dorsal and caudal scales have a row of tubercles. *Coccoderma*, from the Kimeridgian of Europe, is allied to the last. Finally, *Macropoma* (fig. 910), from the Chalk, comprises several large species readily characterised by the notochord not extending to the extremity of the tail.

Family Polypteridæ.—The last family of the suborder is known only by the existing African genera *Polypterus* (fig. 906, A) and *Calamoichthys*, each of which is represented by a single species. The vertebral column is ossified; the dorsal fin broken up into a number of small finlets; the pectorals are obtusely lobate; the caudal fin is diphycercal, with a very short body-axis; and the scales are rhomboidal.

Suborder 5. Acipenseroidea.—According to the views of Dr Traquair, the Acipenseroids, represented typically by the Sturgeons and their allies, and forming the Chondrostei of many authors, are also taken to include the Heterocerci, as represented by the extinct *Palæoniscidæ*. The following are some of the leading features of the group as thus defined. The paired fins are non-lobate; the pectoral girdle, which in the typical forms retains its primitive endoskeletal cartilages, develops dermal bones, among which the infraclavicular (fig. 913) is characteristic; the dermal rays of the dorsal and anal fins are more numerous than their supporting cartilages, or interspinals, of the endoskeleton; while in the paired fins these dermal rays have to a great extent replaced the original cartilages. In the skull the cartilaginous cranium persists in the typical forms, but in all cases it is overlain by a series of dermal bones; the preopercular, when present, tends to extend on to the cheek; branchiostegal rays are generally present; but there are never large jugular plates. The notochord is persistent, but there are either cartilaginous or bony neural and hæmal arches; the tail is heterocercal, and the skin may be either naked, or dotted over with bony scutes, or covered with rhomboidal scales.

Mr Smith Woodward remarks that the typical forms of this suborder constitute a link connecting the cartilaginous Ganoids with these fishes in which the bones are fully developed, and that their paired fins are more specialised than the median ones, which have not yet attained a numerical equality between the fin-rays and their supporting interspinals.

Family Acipenseridæ.—The well-known Sturgeons (fig. 911), which form the typical family, are large fresh-water fishes, characterised by their elongated body, produced snout, toothless jaws of

the adult, the presence of five rows of scutes formed of true bone on the body, and the sculptured cranial bones. The representatives of the existing genera *Acipenser* (fig. 911) and *Scaphirhynchus* are found in many of the larger rivers of the Northern Hemisphere. Scutes referred to *Acipenser* occur in the London Clay, and in some higher Tertiary beds; while spines from the English Upper Eocene

Fig. 911.—The Sturgeon (*Acipenser sturio*). Much reduced.

and the Pliocene of Montpellier probably also belong to the same genus. A single scute has also been described from the Miocene of Virginia under the same name.

Family Polyodontidæ.—In this family, now represented by *Polyodon* of the Mississippi and *Psephurus* of two rivers in China, the skin is typically nearly or quite naked, the mouth is of enormous width, and the jaws carry minute teeth. In a fossil state this family is represented by *Crossopholis*, from the Eocene of Wyoming, which displays many points of resemblance to *Polyodon*, but is remarkable for the possession of small pectinated scales, which are not confined to the upper lobe of the tail. The cranial bones are of the type of those of *Polyodon*, but the shorter rostrum indicates a resemblance to *Psephurus*. The scales are numerous, and are arranged in oblique rows, which are not quite in contact with one another. The retention of the scales in this genus indicates that we have to do with a much less specialised member of the family than the existing forms. The genus *Macropetalichthys*, from the Devonian of both North America and the Eifel, has frequently been referred to the *Polyodontidæ*, but without any sufficient evidence, and its serial position must for the present remain undetermined. The cranium (fig. 912) is short and broad, with the orbits completely surrounded by bone, and the middle line occupied anteriorly by a diamond-shaped ethmoidal shield, which articulates posteriorly with a process from the squared hinder shield.

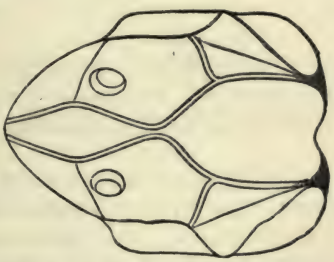

Fig. 912.—Diagram of the frontal aspect of the cranium of *Macropetalichthys Sullivani*; from the Devonian of North America. Much reduced. (After Newberry.)

As an Acipenseroid of uncertain position may also be mentioned the imperfectly known *Pholidurus*, of the English Chalk—the tail of which presents some resemblance to that of *Psephurus*. A huge fish from the English Upper Lias, named *Gyrosteus*, is evidently also an Acipenseroid agreeing with the type genus in the absence of teeth, but having a naked body. It differs also considerably from the type of the next family, and its position must remain uncertain.

Family Chondrosteidæ.—This family is formed for the reception of the one comparatively small fish constituting the genus *Chondrosteus* from the English Lower Lias. According to Dr Traquair, although there is no evidence of a long snout (fig. 913), this genus resembled *Polyodon* in the general form of the fins, and of the nearly naked body; but in other respects—such as the form of the cranial bones and the absence of teeth—approaches *Acipenser*. Certain features also appear to indicate distinct affinity with the

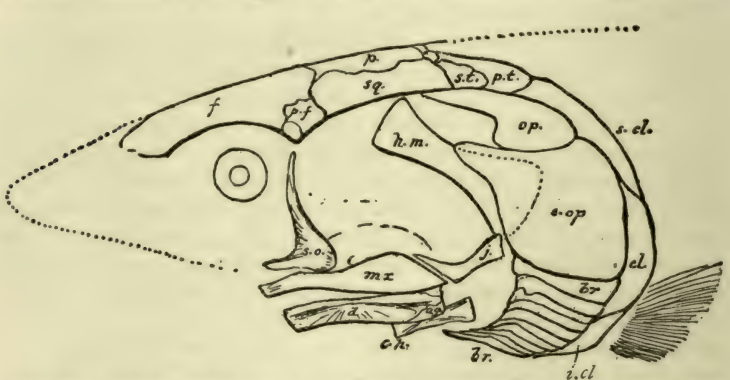

Fig. 913.—Profile view of the head of *Chondrosteus acipenseroides;* from the Lower Lias of Dorsetshire. Reduced. *f*, Frontal; *p.f*, Postfrontal; *p*, Parietal; *sq*, Squamosal; *s.t*, One of the supratemporals; *p.t*, Posttemporal; *s.cl*, Supraclavicular; *cl*, Clavicular; *i.cl*, Infraclavicular; *op*, Opercular; *s.op*, Subopercular; *br*, Branchiostegals; *c.h*, Ceratohyal; *ag*, Angular; *d*, Dentary; *mx*, Maxilla; *j*, Jugal; *h.m*, Hyomandibular; *s.o*, Suborbital. (After Traquair.)

Palæoniscidæ; and since the latter are evidently allied to the higher bony Ganoids, Mr Woodward suggests that they or allied forms may have given origin to two series, one of which culminated in the Teleosteans, while in the other "the only advance has been in the matter of size, and this accompanied by a certain amount of degeneration, culminating in Acipenseroids proper."

Family Palæoniscidæ.—This and the next family constitute the suborder Heterocerci of some writers. In the present family the body is fusiform, and covered with rhomboidal scales; the vertebral arches are ossified, but there are no bony ribs; the dorsal fin is single and short; all the fins have large fulcra at their bases; the

cranial bones are covered with ganoine, and mostly sculptured; the mouth is large; the first branchiostegal rays form jugular plates; there is a row of median V-shaped scales on the superior surface of the extremity of the body; and the teeth are small, conical, or cylin-

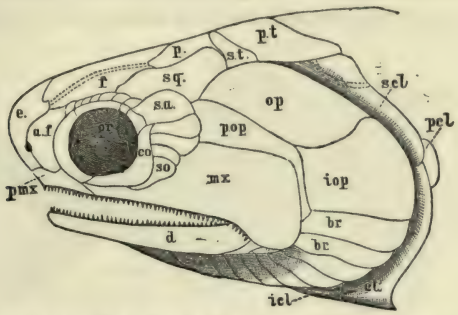

Fig. 914.—Left lateral view of the skull of *Palæoniscus macropomus;* from the Permian. *p*, Parietal; *f*, Frontal; *sq*, Squamosal; *s.t*, Supratemporal; *p.t*, Posttemporal; *e*, Ethmoid; *a.f*, Prefrontal; *pmx*, Premaxilla; *mx*, Maxilla; *co*, *sa*, *so*, Suborbitals; *d*, Dentary; *op*, Opercular; *p.op*, Preopercular; *iop*, Subopercular; *br*, Branchiostegals; *cl*, Clavicular; *scl*, Supraclavicular; *pcl*, Postclavicular; *icl*, Infraclavicular; *or*, Orbit. (After Traquair.)

drical, and rarely plicate at the base. The chief characters of the bones of the skull and of the secondary pectoral girdle are shown in fig. 914, in which it will be seen that the preopercular covers a portion of the face above the large and broad maxilla. Dr Traquair observes that if a Palæoniscid were stripped of its scales and furnished with a long snout, it would be so like *Polyodon* that there would be no doubt as to their near relationship; and he further remarks that the one row of V-shaped scales found on the dorsal side of the extremity of the body in *Polyodon* is identical with the row of scales occupying the same position in *Palæoniscus*. This leads to the conclusion that the existing Sturgeons are the survivors of a series of Ganoids, now totally lost, which formerly gave off the *Palæoniscidæ* and *Platysomidæ* as specialised branches.

This family embraces such a large number of genera, that space permits of but little more than their bare enumeration. In the Devonian *Chirolepis*, found both in Europe and Canada, the body is slender, and the fins are large, with the rays very finely divided; while *Rhabdolepis* (fig. 915) of the Rothliegendes (Lower Permian), while having fins of somewhat similar structure, is distinguished by the deeper and more spindle-shaped body. *Cosmoptychius*, of the Scotch Carboniferous, is allied to *Rhabdolepis*, but has the anal fin with a longer base. In the type genus *Palæoniscus* (figs. 914, 916) the body is much elongated, and the fins are very small and widely separated. It occurs in the Kupfer-Schiefer and Magnesian Lime-

stone (Middle Permian) of Germany and England; and one species has been said to occur in the English Trias. That species is, however, now referred to the *Dapediidæ;* but a true *Palæoniscus* is recorded from the Hawkesbury beds of New South Wales, which may be of Triassic age. The remaining better known genera are *Elonichthys*, from the Carboniferous of Europe and America; *Acro-*

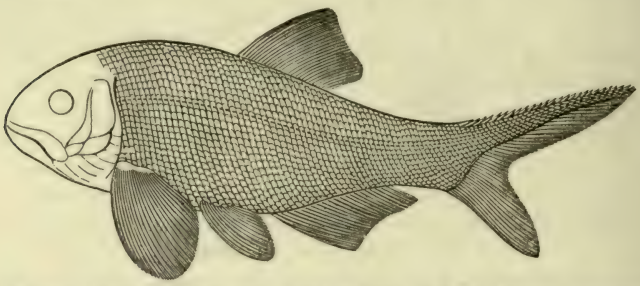

Fig. 915.—*Rhabdolepis macroptera;* from the Lower Permian of Saxony. Reduced. (After Agassiz.)

lepis, ranging from the Permian to the Carboniferous, and perhaps to the Devonian, of Europe; *Nematoptychius*, *Cycloptychius*, *Micronodus*, and *Gonatodus*, from the British Carboniferous; the gigantic *Amblypterus*, of the German Permian; *Rhadinichthys*, from the Carboniferous of both Europe and North America; *Eurylepis*, from the Carboniferous of Ohio; *Holurus*, *Canobius*, and *Phanerosteon*, of the Scottish Carboniferous; *Pygopterus*, of the German Permian; *Myriolepis*, from the Hawkesbury of New South Wales; *Urosthenes*, from the underlying Newcastle group of the latter country; *Gyro-*

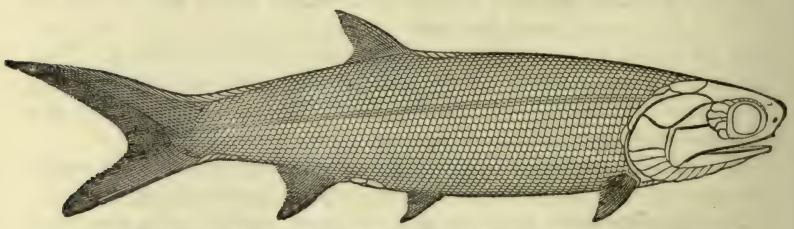

Fig. 916.—*Palæoniscus macropomus;* from the Middle Permian of Germany. Reduced. (After Traquair.)

lepis, from the Middle Trias of the Continent; and *Oxygnathus*, *Cosmolepis*, *Thrissolepis*, *Centrolepis*, and *Lissolepis*, from the English Lias. Here also may be mentioned the genera *Sphærolepis*, of the Permian of Bohemia, and *Coccolepis*, of the Kimeridgian of Bavaria, which, although having cycloidal imbricating scales, appear to be allied to the present family.

Family Platysomidæ.—The *Platysomidæ* agree with the preceding family in the characters of the vertebral column, fins, scales, and the main cranial structure, but differ by the body becoming deep and short, with an ovoid or rhomboidal contour, and also by minor modifications in the cranial structure. The teeth are small, and may be either sharp or obtuse. The chief difference in the structure of the skull consists in the deflection of its axis below that of the vertebral column, instead of being continuous; while the hyomandibular, instead of being very oblique, becomes nearly vertical, and the ethmoid is elongated. These changes cause the mouth to be separated widely from the orbit, the jaws to become "prognathous," and the gape of the mouth itself to be much reduced; they are readily apparent by contrasting the figure of *Palæoniscus* with that of *Chirodus*. Dr Traquair regards this family as a group of specialised forms descended from the *Palæoniscidæ;* their external resemblance to the *Dapediidæ* being probably due merely to adaptation to similar conditions of life, and not indicating a real affinity. In *Eurynotus* (fig. 917) the contour of the body is not so greatly

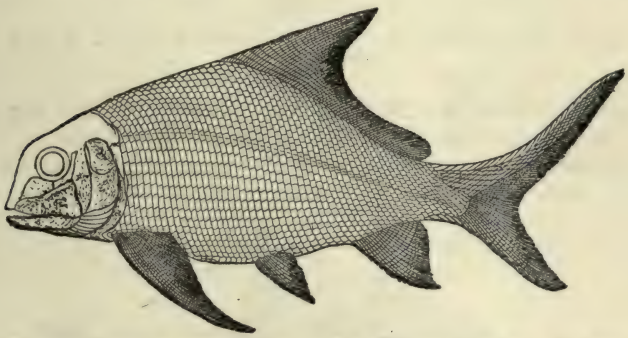

Fig. 917.—*Eurynotus crenatus;* from the Carboniferous of Scotland. Reduced. (After Traquair.)

removed from the Palæoniscid type; the pectoral fin is large, the dorsal also large, and beginning above the pelvic, while the base of the anal is short. This genus occurs in the Carboniferous of Scotland and Belgium. In *Benedenius*, of the Belgian Carboniferous, the body becomes more oval, and the dorsal fin is placed more posteriorly. More or less nearly allied to this group are *Mesolepis*, of the British Carboniferous; *Eurysomus*, of the Middle Permian of England and Belgium; and *Wardichthys*, of the Scottish Carboniferous. In *Chirodus* (fig. 918), of the British Carboniferous, the body is rhomboidal; the dorsal and anal fins have a long base, short rays, and an anterior spine; while the pelvic fin is unknown, and the pectoral small. Closely allied, again, is *Chirodopsis*, from

the same horizon. The last and type genus *Platysomus* (figs. 919 and 920) is represented by a large number of species, ranging from the Carboniferous of England and North America to the Middle

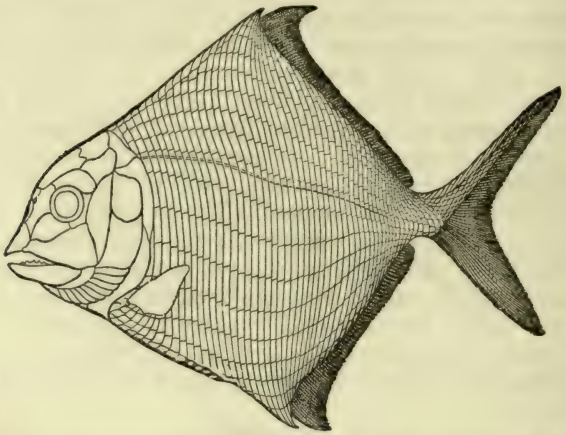

Fig. 918.—*Chirodus granulosus;* from the Carboniferous of Scotland. Reduced. (After Traquair.)

Permian of England and the Continent. The contour of the body is less rhomboidal than in *Chirodus;* the dorsal and anal fins have no anterior spines; the pelvic fin is very small, and but seldom preserved; while the pectoral is of medium size.

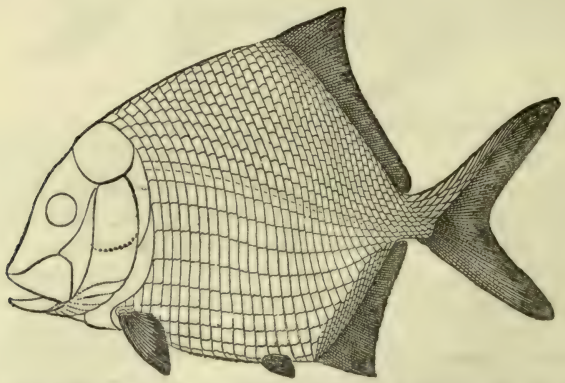

Fig. 919.—*Platysomus striatus;* from the Middle Permian of England. Reduced. (After Traquair.)

Suborder 6. Lepidosteoidea.—In the Lepidosteoids the paired fins are non-lobate; there is no infraclavicular bone; the rays of

the dorsal and anal fins correspond in number with their supporting interspinous bones; the opercular bones are like those of the Teleostei; there is frequently a median jugular plate on the first pair of branchiostegals; the development of the vertebral column varies; the tail is of the masked heterocercal type; and the scales are rhomboidal, or may be occasionally replaced by angular scutes. This

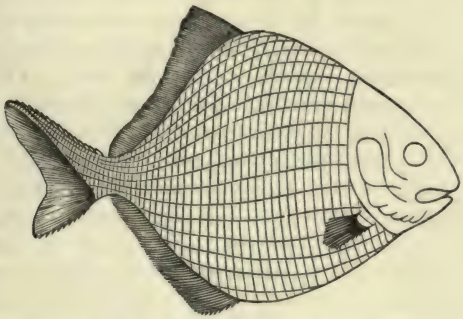

Fig. 920.—*Platysomus gibbosus*; from the Middle Permian of Germany. Reduced. The pelvic fin is not shown.

suborder is represented at the present day by the somewhat aberrant *Lepidosteidæ*, and also by a large number of Mesozoic forms ranging from the Trias upwards. As already mentioned, the external resemblance of the *Dapediidæ* and *Pycnodontidæ* to the *Platysomidæ* is not regarded by Dr Traquair as indicative of real affinity.

Family Dapediidæ.—In this family, which by some writers is subdivided and known as the *Sauridæ* and *Stylodontidæ*, the body is either fusiform or ovate; the opercular bones present certain

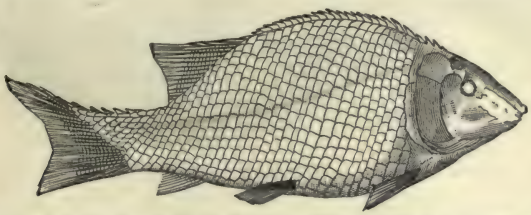

Fig 921.—*Semionotus Kapffi*; from the Keuper of Würtemberg. (After Fraas.)

characteristic features; the upper lobe of the body-axis of the tail, and usually the anterior borders of the other fins, have well-developed fulcra; the vomer and jaws carry several rows of small teeth, of which the outermost are curved and resemble claws (*griffelzahne*); and the ossification of the vertebral column is imperfect. Among the genera with fusiform bodies, one of the best known is *Semionotus*

(fig. 921), which is widely spread over Europe. According to Dr Deecke, this genus is represented in the Bunter and Muschelkalk; it is common in the Keuper, or Upper Trias, and thence ranges to the Kimeridgian, or Upper Jurassic. It has also been recorded from the Stormberg beds in the upper part of the Karoo system of South Africa; and it appears to be also represented in the Trias of North America, where it has received the name of *Ischypterus*. In these fishes the dorsal fin is small, the inequality of the scaled portion of the caudal strongly marked, and there is a row of large spine-like scales on the middle line of the back. Other more or less nearly allied forms, of which some were formerly included in *Palæoniscus*, are *Acentrophorus*, from the British Permian; *Catopterus*, from the North American Trias; and *Dictyopyge*, from the Trias of both England and North America, the type species of the latter having been originally named *Palæoniscus superstes*. In *Heterolepidotus*, typically from the Lower Lias of England, and *Heterostrophus*, from the Kimeridgian of Bavaria, we have genera in which the contour of the body is more like that of the type genus. *Heterolepidotus*, according to Dr Deecke, is also represented in the Muschelkalk, and survived to the Kimeridgian. The name *Allo-*

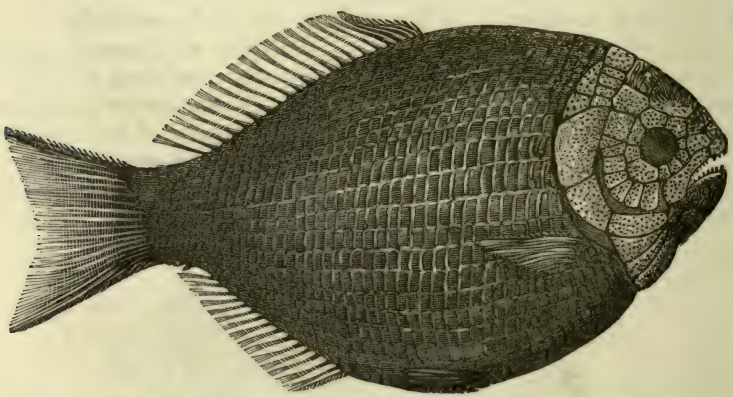

Fig. 922.—*Dapedius pholidotus*; from the Upper Lias of Würtemberg. Reduced.

lepidotus is applied to allied types also represented in the Muschelkalk. *Dapedius* (fig. 922), in which *Æchmodus* may be included, comprises a number of medium-sized fishes with broadly ovate bodies, ranging in Europe from the Keuper to the Lower Jurassic, but also occurring in the Kota beds of the Indian Gondwanas, which are somewhat higher than the Maleri beds from which *Ceratodus* is obtained. The dorsal and anal fins have elongated bases, and the inequality between the upper and lower lobes of the scaled part of

the caudal fin is comparatively slight. In typical species the teeth are simple, while in others (on which *Æchmodus* was founded) they are forked at their summit; since, however, both types are occasionally found in a single species, they do not afford grounds for generic distinction. The so-called *Amblyurus* has been founded on crushed Liassic specimens of *Dapedius*. Allied forms are *Pleurolepis* and *Homœolepis*, from the Upper Lias of Würtemberg. In *Tetragonolepis*, of the European Lias and the Kota beds of the Indian Gondwanas, the body resembles that of the type genus, but the form of the dorsal and anal fins is different, the caudal fin is nearly symmetrical, and the vertebral centra develop rings of bone; all these characters approximating to the next family, in which Sir P. Egerton placed both this and the following genus. *Clithrolepis* is an allied genus typically from the Wianumattu and Hawkesbury beds of New South Wales, but also occurring in the Stormberg beds of the South African Karoo system, and not improbably in the Indian Kota beds; all these strata being of approximately equivalent age.

Family Pycnodontidæ.—The Pycnodonts form a compact group, ranging from the Lias to the Eocene, in regard to the serial

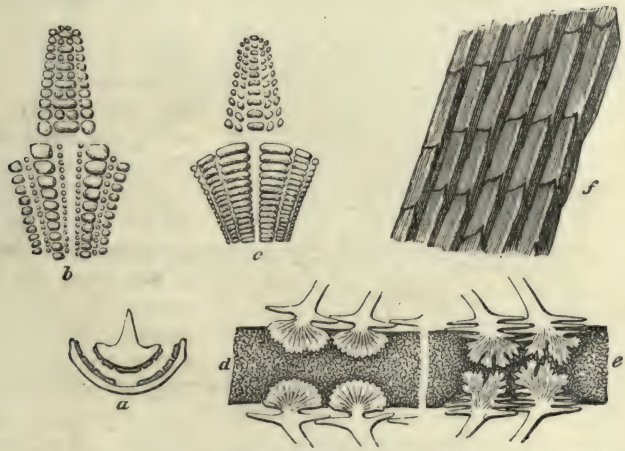

Fig. 923.—Dentition, scales, and vertebral column of Pycnodonts: *a*, Jaws, and *b*, vomerine and mandibular teeth of *Microdon*; *c*, Do. of *Cœlodus*; *d*, Vertebral column of *Palæobalistum*; *e*, Do. of *Pycnodus*; *f*, Scales of *Gyrodus*. The dentition is greatly reduced.

position of which very divergent views have been entertained. Dr Traquair is, however, disposed to regard them as specialised forms connected with the *Dapediidæ* and *Lepidotidæ*, and they are accordingly here placed between those families. This family has been recorded from Europe, Asia Minor, North America, and Australia, and presents the following characteristics. The body is of a rhomb-

oidal shape, presenting a striking resemblance in this respect to the *Platysomidæ;* the caudal fin is of a completely masked heterocercal type, and there are no fulcra to the fins. The notochord is persistent, but the neural arches and ribs are ossified, and in the later forms the heads of the latter (fig. 923) are enlarged, so as to simulate portions of vertebral centra. The premaxillæ are toothless; the conjoint palatines and vomer form a triangular bone (fig. 923), carrying five longitudinal rows of oval or round molariform teeth, while in the mandible the dentary bones, which form the extremity of the symphysis, have two or four chisel-like teeth, and the splenials are enlarged and carry on either side from three to five or more rows of molariform teeth (fig. 923) opposed to those of the former. Commencing with the typical genus *Pycnodus*, we find this, as now defined, restricted in Europe to the Lower Eocene of Sheppey and the Middle Eocene of Monte Bolca in Italy. There are only three rows of teeth on either side of the mandible, of which the innermost is the largest; while on the vomer the teeth of the three inner rows are round, and those of the two outer rows are larger and oval. Other characters are found in the position of the orbit, the large size of the mouth, and the superiority in the length of the dorsal as compared with the anal fin. A fish from the Cretaceous of Brazil has been referred by Professor Cope to this genus. The allied *Palæobalistum* (fig. 923, *d*), in which all the upper teeth are subequal, occurs in the Chalk of the Lebanon, the Cretaceous Pisolite of Mont Aimé in France, and also in the Middle Eocene of Monte Bolca. The greater number of the Cretaceous forms are, however, referable to the genus *Acrotemnus Cœlodus*,[1] which comprises some species attaining

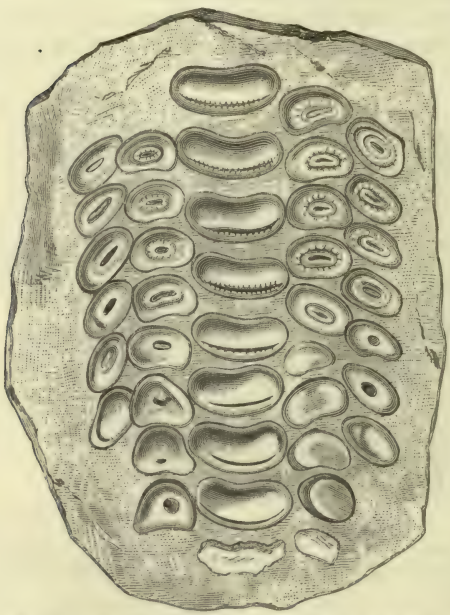

Fig. 924.—Vomer of *Acrotemnus gyrodoides;* from the English Cretaceous. (After Egerton.)

[1] The name *Cœlodus* being preoccupied by *Cœlodon*, the term *Acrotemnus*, proposed by Agassiz for detached teeth, is adopted.

a large size. The vomerine teeth (fig. 924) of the middle row are elliptical, and much larger than either of the others, while there are usually three rows on either side of the mandible, although these are occasionally increased to four. The dorsal fin extends in advance of the anal. This genus ranges from the Gault to the Chalk, and is widely spread through Europe. In *Mesodon* we have a genus ranging from the English Lias to the Lower Kimeridgian of Bavaria, and not improbably also represented in the Lower Greensand. Here the vomerine teeth of the middle row are larger than the teeth of the other rows, which are exceedingly small, and in the outermost line have a wart-like surface. Allied genera are *Mesturus* and *Athrodon* from the Kimeridgian of the Continent.

Stemmatodus (fig. 925), which comprises two small species from the Lower Cretaceous of Italy, is characterised by the great length

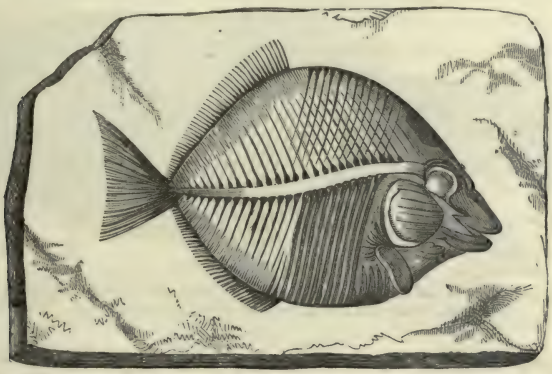

Fig. 925.—*Stemmatodus rhombus;* from the Lower Cretaceous of Italy.

of the dorsal and anal fins, and also by the concave surfaces of the molariform teeth, which are of subequal size. *Microdon* is another allied genus, ranging in Europe from the Kimeridge to the Purbeck. The arrangement of the teeth, and the peculiar structure of the heads of the ribs are shown in fig. 923. In *Gyrodus* we seem to have the most specialised members of the entire family, all of them being characterised by the sculptured crowns of the molariform teeth. The vomer is very narrow, and has the teeth subcircular, those of the middle row being much the largest; while in the mandible there are four rows on either side, of which the first and third are the larger. This genus is especially abundant in the Lower Kimeridgian lithographic limestone of Bavaria, but it also ranges upwards into the Chalk of Sussex, and downwards into the Lower Jurassic Stonesfield Slate. Finally, *Coccodus* is founded on an imperfect specimen from the Chalk of the Lebanon really belonging

to this family, but which has been referred to the Teleostean Siluroids.

Family Lepidotidæ (Sphærodontidæ).—In the *Lepidotidæ* the body is more or less fusiform, the upper scaled portion of the tail is longer than the lower, and the fulcra of the fins are well developed. The palatine, vomer, maxilla, and dentary carry rows of knob-like teeth (fig. 926), while the premaxilla is furnished with teeth of a chisel-like form. The type genus *Lepidotus* (fig. 926), with which *Sphærodus* is in great part identical, has a wide distribution both in time and space. Thus, in Europe it ranges from the Muschelkalk, or Middle Trias (where its scales have been described under the names of *Dactylolepis* and *Thollodus*) to the Chalk, and it also occurs in the Kota group of India, and the Cretaceous of Brazil and of North America. The large button-like teeth of *L. maximus* are abundant in the Kimeridge Clay, and specimens have been

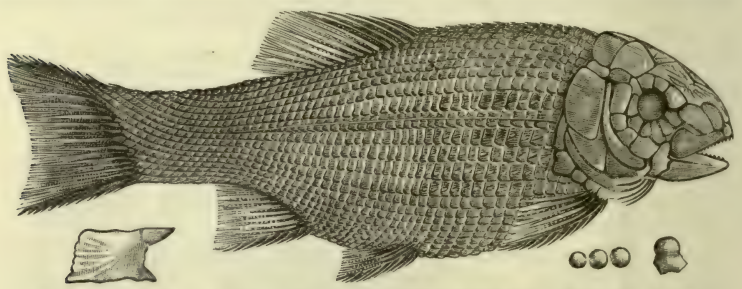

Fig. 926.—*Lepidotus maximus*; from the Kimeridgian of Bavaria. Reduced. Larger views of teeth and a scale are given in the corners.

found comprising nearly the whole palate, and exhibiting the curious manner in which the replacing teeth gradually turn over as they come into use. The names *Nephrotus*, *Cenerodus*, *Omphælodus*, *Hemilopus*, and *Asterodon*, have been applied to molariform and chisel-like teeth belonging to members of this family from the Trias of Silesia and Thuringia; while teeth of the latter type from the bone-bed of the same period, in both Würtemberg and England, described under the name of *Sargodon*, should, perhaps, be likewise placed here; and *Neorhombolepis*, of the English Chalk, appears to be an allied form.

Family Eugnathidæ (Saurodontidæ).—The body in this family is long and slender; the snout short; the fins have fulcra, the caudal being of a partially or completely masked heterocercal type; the vertebral centra may be either imperfectly or fully ossified, and the teeth are pointed. The range in time of this family extends from the Upper Trias to the Neocomian of Europe, but may, perhaps, also include the Chalk. In the typical group we have *Eu-*

gnathus ranging from the Keuper to the Kimeridgian, while in the Lias we find *Platysiagum* and *Ptycholepis*, and *Pholidopleurus* and *Peltopleurus* in the Keuper. A second group is represented by *Pleuropholis*, of the Kimeridgian of Bavaria, and also by *Thoracopterus* and *Pterygopterus* of the Keuper, the latter being distinguished by the absence of the pelvic fins. The genus *Pholidophorus* includes small Fishes somewhat resembling a Carp in form, which range from the Muschelkalk to the Purbeck. A fish from the Muschelkalk, originally described as *Pholidophorus porro*, has been made the type of the genus *Prohalecites*, on account of peculiar features in its squamation. Larger forms are ranked under the genera *Isopholis* of the Lias and Kimeridgian, and *Ophiopsis*, which extends from the Lias to the Purbeck. Of the remaining genera we have *Eusemius* and *Propterus* in the Kimeridgian of Bavaria; *Notagogus* from the latter deposits, and also in the Lower Greensand of Italy; *Histionotus* in the Bavarian Kimeridgian and the English Purbeck; *Macrosemius* ranging from the Stonesfield Slate to the Kimeridgian of Bavaria; and *Legnonotus* from the English Lias. *Lophiostomus*, from the Chalk of Sussex, may perhaps be placed here, although its skull approximates to that of *Amia*. The scales are pitted, and have a pectinated posterior border.

Family Aspidorhynchidæ (Rhynchodontidæ).—In this family the body is much elongated, and covered with scales of unequal

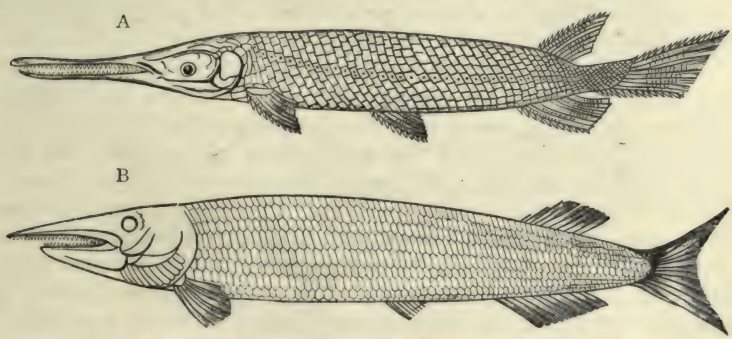

Fig. 927.—A, The Gar-pike (*Lepidosteus osseus*). Recent. North America. B, *Aspidorhynchus*; from the Jurassic. Both much reduced.

sizes; the skull is produced into a short rostrum; the caudal fin is of the masked heterocercal type; the fins carry fulcra; the vertebræ have ossified rings; and the teeth are either blunt or sharp. This family is represented only by the Mesozoic genera *Aspidorhynchus* and *Belonostomus*, in both of which the dorsal fin is placed above the anal. In the former (fig. 927, B), which ranges from the Lias to

the Purbeck, the length of the upper jaw exceeds that of the lower, and in advance of the mandibular symphysis there is a predentary bone (not shown in the figure) apparently corresponding to the one found in certain Dinosaurs. In *Belonostomus*, which, as now restricted, ranges from the Lower Kimeridgian of Bavaria to the Chalk, the predentary bone is so much elongated as to make the upper and lower jaws of nearly equal length, and the predentary carries a median row of large conical teeth, flanked by two rows of minute teeth; the teeth of the normal bones of the jaws having mammilated crowns adapted for crushing.

Family Belonorhynchidæ.—This family name has been proposed by Mr S. Woodward for the remarkable genus *Belonorhynchus*, typically occurring in the Upper Trias of Carinthia, but also found in the Lower Lias of Dorsetshire, where the specimens had been originally referred to *Belonostomus*. According to the writer quoted, *Belonorhynchus* was allied to the latter genus, having a similar long and slender body, with the same general position and structure of the fins, and probably furnished with a predentary bone. The fulcra of the fins were, however, either absent or very minute; and, with the exception of a median dorsal and ventral series of scutes, and another series on the lateral line, the body was naked. The imperfectly known *Saurichthys*, from the Rhætic of Bristol, is a closely allied, if not generically identical, type. Specimens of the upper jaw show that (as in *Belonorhynchus*) the bone was covered with fine tubercles, and that the maxillæ gave off horizontal palatal plates, like those found in Amphibians and Reptiles.

Family Lepidosteidæ.—The Gar-pikes of the genus *Lepidosteus* (fig. 927, A), inhabiting the freshwaters of Northern and Central America and Cuba, agree with the *Aspidorhynchidæ* in the general contour of the body and the arrangement of the fins; but the rostrum of the skull is much longer, and the tail distinctly heterocercal. The scales are lozenge-shaped. The existing genus appears to be represented in the Lower Eocene of France by a species (*L. Maximiliani*) formerly referred to *Lepidotus;* and it may also occur in the Upper Eocene (Oligocene), where a species described under the name of *Naisia* has been referred to it. In North America we have also *Pneumatosteus*, from the Miocene, and *Clastes*, from the Lower Eocene, both being freshwater forms, and the latter also occurring in the Eocene of Rheims.

Suborder 7. Amioidea.—According to Dr Traquair's classification, the last and most specialised suborder of the Ganoids is typically represented by the existing *Amia* and a series of Mesozoic genera approximating more or less closely to the Teleostei. In these forms the paired fins are non-lobate; the infraclavicular bone is absent; the opercular are Teleostean; the branchiostegals have a

median jugular plate; the vertebræ are more or less completely ossified; the tail is masked heterocercal; and the scales are thin and usually cycloidal. In all cases the teeth are small and pointed. It is probable, indeed, that in the Mesozoic representatives of this group we have forms closely allied to the ancestors of the Teleostei, and it is more than likely that future discoveries will show a complete passage between the Ganoids, as represented by this suborder, and the Teleosteans.

Family Pachycormidæ (Microlepidoti).—According to Professor Zittel, *Pachycormus* and its allies should be placed in this suborder, although other writers have regarded them as more nearly related to the *Dapediidæ*. In these forms the scales, although thin and imbricating, are subrhomboidal, and the vertebral column is very incompletely ossified. The chief genera, which are European, include *Pachycormus*, ranging from the Lias to the Oxford Clay (Middle Jurassic); *Endactis*, from the Lower Lias; *Euthynotus*, of the same horizon; and *Hypsicormus*, *Sauropsis*, and *Agassizia*, of the Lower Kimeridgian of Bavaria.

Family Caturidæ.—The Caturoids are a family of Salmon-shaped fishes, varying greatly in size, and ranging in time from the Lias to the Chalk, but especially common in the Kimeridgian lithographic limestones. The vertebral column may be either very imperfectly or completely ossified, the tail is more or less deeply forked, and the fins have fulcra. *Caturus* itself comprises a number of species, some of which are of large size, and two of which are represented in figs. 928, 928 *bis*. The scales are very like those of the Teleosteans,

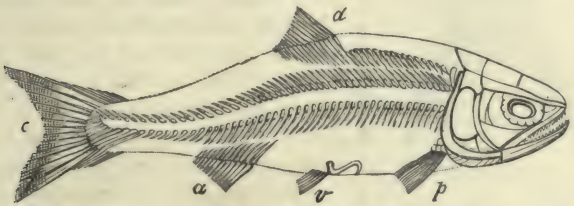

Fig. 928.—Skeleton of *Caturus furcatus*; from the Kimeridgian of Bavaria. Reduced. *p*, Pectoral; *v*, Pelvic; *a*, Anal; *c*, Caudal; *d*, Dorsal fin.

but still retain the Ganoid character of an inferior layer of bone and an upper one of enamel. The dorsal fin is placed immediately above the pelvic. This genus ranges from the Lias to the Kimeridgian, *C. maximus* attaining a length of three feet. *Strobilodus*, from the Kimeridgian of England and the Continent, is a closely allied if not identical genus. Other genera are *Isocolum*, from the Dorsetshire Lower Lias; and the Jurassic *Liodesmus*, *Eurycormus*, *Oligopleurus*, *Œnoscopus* (*Attakeopsis*), *Macrorhipis*, and *Æthalion*. *Oligopleurus*

has the dorsal fin placed behind the pelvic; and in this and several of the other genera the vertebræ consist of the upper and lower horse-shoe-shaped elements mentioned in the preliminary notice of the order.

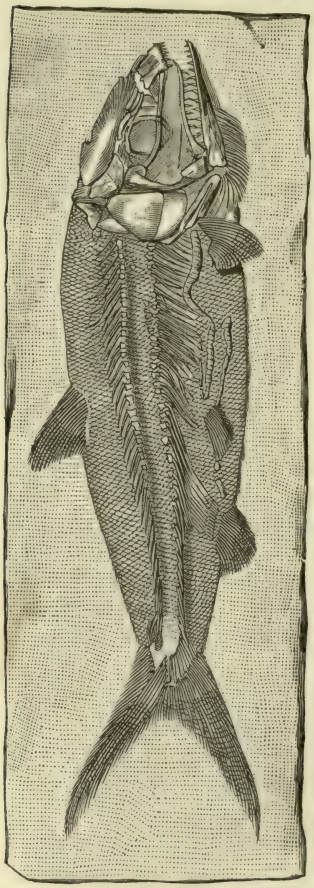

Fig. 928 *bis.* — Skeleton of *Caturus elongatus*; from the Kimeridgian of France. One-half natural size. (After Zittel.)

Family Leptolepididæ.—Of striking similarity in external contour to the Caturoids is the genus *Leptolepis* (fig. 929), which is placed by Dr Günther next to that family, although some palæontologists regard it as a Teleostean. The vertebral column is fully ossified, and the fins are without fulcra. In this genus, which ranges from the Lias to the Kimeridgian, the dorsal fin is placed immediately over the pelvic; but in *Thrissops*, of the Kimeridgian, it is above the anal. In external characters these Fishes cannot be distinguished from Teleosteans; and it is probable that they are intimately connected with that order, even if they should not be placed in it.

Family Amiidæ.—In the Amioids the vertebral column is fully ossified, and in the caudal region has a series of centra bearing the neural and hæmal arches, which alternate with intercentra devoid of such appendages. Fulcra may or not be present; and the caudal fin is convex, with the extremity of the vertebral column bent sharply up into the upper lobe. In *Megalurus*, of the Purbeck and Kimeridgian, fulcra are present, and the dorsal fin is short, and does not extend in advance of the pelvic. *Lophiurus*, from the same horizon, and *Opsigonus* and *Amiopsis*, of the Lower Chalk, are other genera, of which the first two are nearly related to *Megalurus*. The existing *Amia*, of the freshwaters of the southern United States, has no fulcra, and the dorsal fin occupies three-quarters of the length of the body. It appears probable that this genus is represented in the Upper Eocene (Lower Oligocene) and the Lower Miocene of the Continent, where its remains have been

described under the names of *Cyclurus* and *Notæus;* and it also occurs in the Eocene of Colorado and Wyoming, where it has been described as *Protamia* and *Hypamia.* The Eocenes of the latter district and of Rheims have also yielded the allied *Pappichthys*,

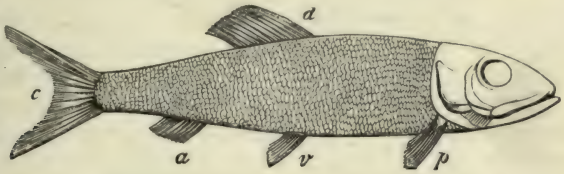

Fig. 929.—*Leptolepis sprattiformis;* from the Kimeridgian of Bohemia. Letters as in fig. 928.

in which there is but a single row of teeth; and members of this family may occur in the Chalk of the Lebanon.

Incertæ Sedis.—The remarkable genus *Dorypterus*, of the Permian of Hesse and Durham, may be conveniently noticed here, since its position is very problematical. In this remarkable fish the body is shaped somewhat like that of a Sunfish, and the anterior part of the dorsal fin is taller than the whole depth of the body. There are, moreover, the Ganoid characters of fulcra to the fins, and the notochordal condition of the vertebral column; but, on the other hand, there are no ganoid scales, and the pelvic fins are placed in advance of the pectorals, as in some of the Teleostei. On account of this curious combination of characters, Professor Cope has proposed to make *Dorypterus* the type of a special order, the Dorycopteri, with the family *Dorypteridæ.*

CHAPTER L.

CLASS PISCES—continued.

Order Teleostei.

Order VI. Teleostei. — The last, and in many respects the most highly organised, order of Fishes is the Teleostei, which includes the greater number of existing forms, and (unless some of the genera here placed in the Amioidea belong to it) does not date back beyond the Cretaceous. The Teleostei are in all probability descended from the Ganoids, and occupy in the class a somewhat analogous position to that held by the Squamata among the Reptiles and the Passeres among Birds; all traces of Amphibian affinities having been entirely lost in this order.

It is impossible to give a definition of the order by which it can be sharply separated from the Ganoids, but the following are its most characteristic features from a palæontological point of view. The body is usually covered with thin elastic, cycloid, or ctenoid scales (figs. 832, 833); but bony scutes or ganoid scales are occasionally present. The whole of the endoskeleton is well ossified; and the gills are freely suspended in a gill-cavity covered by a well-developed operculum (fig. 930). The caudal fin of the adult is of that completely masked heterocercal type usually termed homocercal (fig. 931). The pelvic fins may be either abdominal

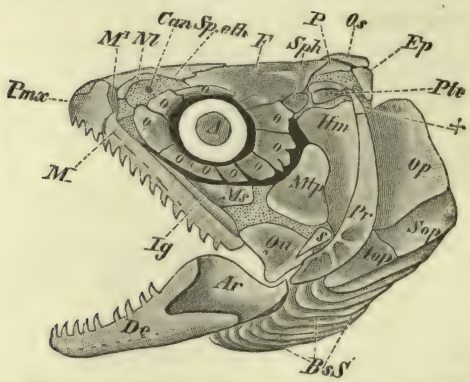

Fig. 930.—Skull of Trout (*Salmo*). Reduced. Letters as in fig. 843, p. 917.

or placed in advance of the pectorals. The fin-rays may or may not be articulated; and there are never fulcra on the fins. There are two pairs of nasal openings on the top of the head. Other characters are found in the soft parts which are not usually available in the case of fossils.

It may further be observed that Teleosteans agree with Ganoids in the hyostylic structure of the skull, and that cranial bones and a secondary pectoral girdle (fig. 844) are always developed. The arrangement of the cranial bones in a typical Teleostean is shown in fig. 930, where it will be seen that the preopercular (*Pr*) does not

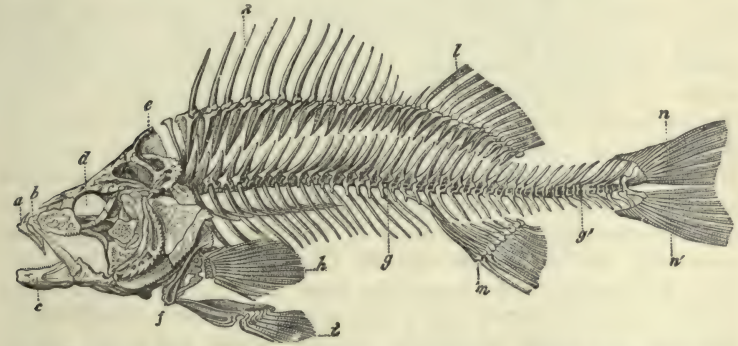

Fig. 931.—Skeleton of the Perch (*Perca fluviatilis*). Reduced. Letters as in fig. 836, p. 913.

extend on to the face as it does in some Ganoids. In certain forms, however (*Siluridæ*), the cranium develops large bony plates, articulating with others in the cervico-dorsal region, and presenting a striking resemblance to some of the cartilaginous Ganoids. In the same group strong spines, articulating with the underlying bones, are developed in the pectoral and dorsal fins; while the Salmonoids, many Siluroids, and others develop behind the rayed dorsal an additional fin without rays, to which the name *adipose* or *fatty fin* is applied.

According to Dr Günther's classification, the Teleostei are divided into six suborders, but other writers would group the last five of these together under the name of Physoclysti, as of equivalent value to the first, or Physostomi. The former arrangement will be followed here, but only such families as are of importance to the palæontologist can be noticed.

Suborder 1. Physostomi.—In this suborder the swim-bladder, when present, is connected by a duct with the pharynx; the pelvic fins are generally abdominal in position, and have no spine; while all the fin-rays are articulated, but sometimes only the first rays of the dorsal and pectoral fins are ossified. This suborder comprises

the most generalised Teleosteans, and those most nearly connected with the bony Ganoids.

Family Salmonidæ.—The members of this and the next family are so intimately connected by fossil forms, that it is very difficult to draw any distinction between them, and it has accordingly been proposed by some writers that they should be united under the name *Halecidæ*. The fossil genus *Halec* is, however, very imperfectly known, and if it be eventually found advisable to merge the two families, it would seem preferable to employ the name *Salmonidæ* in this wider sense. Existing Salmonoids are characterised by the presence of an adipose dorsal fin, and by the premaxilla and maxilla forming the borders of the mouth, and both bearing teeth. There are no scales on the head, and no barbels to the mouth. Recent Salmonoids are either marine, or inhabitants of the freshwaters of the Northern Hemisphere. Remains of the existing marine genus *Osmerus* (Smelt) occur in the Upper Greensand of Germany, the Lower Eocene of Glarus, in Switzerland, and the Miocene of Licata, in Sicily; while nodules of unknown age found in Greenland and Canada enclose a species of *Mallotus* indistinguishable from the existing *M. villosus* of the former region. As forms connecting the Salmonoids with the Clupeoids we may notice *Aulolepis*, *Acrognathus*, and *Osmeroides*, from the English Chalk. The first has a rounded body and a depressed head, with minute teeth, and the pelvic fins abdominal. In the second the orbits are of enormous dimensions, and the teeth extremely minute. The third genus (fig. 932) is also abundantly represented in the Chalk of the Lebanon, and appears to have no adipose fin; its skeleton in many

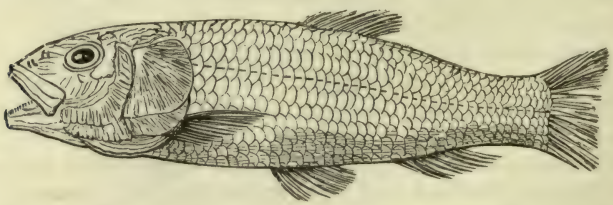

Fig. 932.—*Osmeroides lewesiensis*; from the Chalk of Sussex. Reduced.

respects resembles that of the Clupeoids, but the ribs have not the peculiar structure of that group. *Sardinius*, from the Chalk of the Lebanon, and *Sardinoides* from the same locality, and also from the Chalk of Westphalia, are more or less closely allied forms; while *Opisthopteryx*, of the Lebanon Chalk, may also be provisionally placed here.

Family Clupeidæ.—The existing members of the Clupeoid or Herring family differ from the Salmonoids by the absence of the

adipose fin, and the presence of peculiar dermal ossifications at the ends of the ribs, which form bony plates on the sides of the thorax. All the numerous forms are marine, and usually occur near the coasts. The type genus *Clupea* (Herring) occurs in the Miocene of Würtemberg, the Upper Eocene of the Isle of Wight, the Eocene of Wyoming and Glarus, and the Chalk of the Lebanon. The

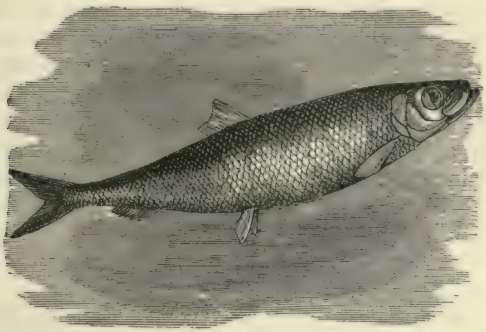

Fig. 933.—The Common Herring (*Clupea harengus*). Reduced.

common existing Herring is shown in fig. 933. The Lebanon Chalk has also yielded a species of the living genus *Engraulis;* and the extinct genera *Scombroclupea*, *Leptosomus*,[1] *Chirocentrites* (also in Westphalia), and *Spaniodon*, which are more or less closely allied to existing types. In the Eocene of the Continent we have representatives of the existing genera *Engraulis* (Anchovy) and *Chanos*, and the extinct *Platinx*, *Cœlogaster*, and *Crossognathus*—the latter being allied to the existing *Megalops*.

In this place we may conveniently notice a number of extinct genera more or less allied to the Clupeoids, but of which the family

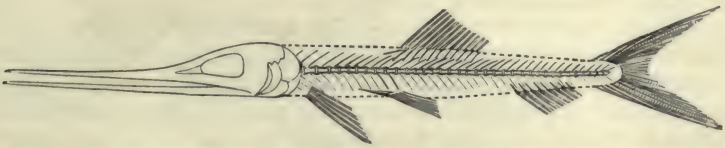

Fig. 934.—Skeleton of *Rhinellus furcatus;* from the Cretaceous of the Lebanon. Reduced. (After Pictet and Humbert.)

position is in some instances uncertain, and some of which retain indications of marked affinities to the higher Ganoids. One of the most remarkable of these is *Rhinellus* (fig. 934), in which the skull

[1] Preoccupied by *Leptosoma*.

is produced into a rostrum, occasionally equal in length to the entire body; this genus occurs in the Chalk of the Lebanon, and is considered to show affinity with *Opisthopteryx*. Another group seems to be related to the existing Clupeoid genus *Elops*, but also presents characters connecting it with the American freshwater family *Characinidæ*. Among these we may notice *Rhacolepis*, from the Cretaceous of Brazil; and in Europe *Elopides*, from the Lower Eocene of Glarus; *Elopopsis*, from the Cretaceous of Bohemia and Istria; *Hemielopopsis*, in which the borders of the mouth appear to have been devoid of teeth, from that of Lesina, on the Dalmatian coast; and *Protelopis*, of the Bohemian Cretaceous, characterised by the short jaws and the presence of crushing-teeth on the palate. *Thrissopater*, again, from the Folkestone Gault, differs from the modern Elopine type by its compressed body; while *Halec*, of the European Chalk, is still very imperfectly known. *Alosa*, of the

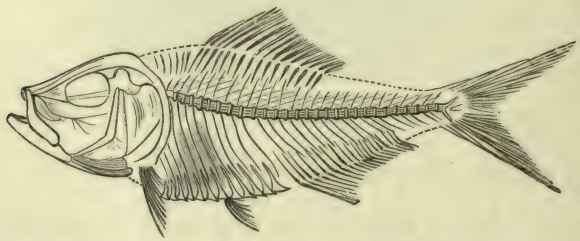

Fig. 935.—Skeleton of *Diplomystus brevissimus*; from the Chalk of the Lebanon.

Eocene of Algeria, and *Diplomystus* (fig. 935), originally described from the Eocene of Wyoming, but subsequently found in the Cretaceous of Brazil and of the Lebanon, are allied forms. The latter genus has a series of dorsal scutes, which are very characteristic. *Hemitrichias*, from the Tertiary of Northern Italy, differs from all existing Clupeoids in having two dorsal fins.

Family Protosphyrænidæ.—With this family we come to the first of a group comprising several families of extinct marine Fishes characterised by their large spear-like teeth, and hence termed Saurodonts. They should evidently be placed near the Clupeoids, although their division into families must be regarded as provisional. The present family is characterised by the production of the ethmoid in advance of the maxilla, to form a long cylindrical rostrum; by the loose connection of the premaxillæ with the maxillæ; and probably also by the complexity of the mandible. The teeth were implanted in distinct sockets. The type genus *Protosphyræna* (*Erisichthe*) occurs in the Upper Cretaceous of both Europe and North America; and the large spear-like teeth of *P. ferox*, which

has the same distribution as the genus, are very common in the coprolitic beds of the Cambridge Greensand, and were for a long time referred to the American *Saurocephalus lanciformis*, which was once thought to be a Reptile. These teeth are compressed, and without marginal serrations. The fins were provided with large ribbed spines, which were at one time referred to the Selachian genus *Ptychodus*, and subsequently were made the type of another genus under the name of *Pelecopterus*.

Family Dercetidæ (Hoplopleuridæ).—The members of the second family of Saurodonts are characterised by their elongated shape, their powerful dentition, and the presence of several series of large triangular scutes along the sides of the body; there is but one dorsal fin in those forms in which the fins are known; the teeth are not implanted in sockets; and the skull is frequently produced into a rostrum. This family probably passes imperceptibly into the next.

The typical genus *Dercetis* (in which *Leptotrachelus* may be included) occurs in the Chalk of England, Bohemia, and the Lebanon, and also in the Upper Cretaceous of Westphalia; it is characterised by the length of the upper jaw exceeding that of the lower, and by the presence of five rows of scutes, of which the middle one bears the lateral line. The allied *Aspidopleurus* is confined to the Lebanon beds. Other members of this family are *Blochius*, from the Middle Eocene of Monte Bolca; *Plinthophorus*, of the English Chalk; *Pelagorhynchus*, from the Upper Cretaceous of Westphalia; and *Saurorhamphus*, from that of Istria. *Plinthophorus* has two rows of scutes, but is otherwise naked.

Family Enchodontidæ.—The genera which may be provisionally grouped under this name are distinguished by the moderate lateral compression of the body, which may be either naked or

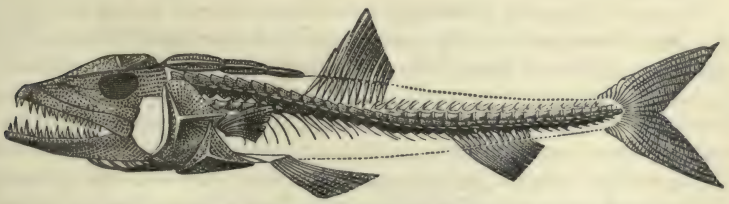

Fig. 936.—Skeleton of *Eurypholis Boissieri*; from the Chalk of the Lebanon. Reduced. (After Pictet and Humbert.)

covered with scutes, and by the elongated premaxillæ and maxillæ, which carry small teeth anchylosed (like those of the mandible) to the bone. A considerable portion of the maxilla is excluded from the margin of the jaw by the premaxilla; teeth occur on the pala-

tines and ectopterygoids; and the dentary bone of the mandible has one series of large teeth, with one or more inner rows of smaller ones. The type genus *Enchodus*, with which *Eurygnathus* of the Lebanon beds is identical, occurs in the Upper Cretaceous of Europe, North America, Brazil, and perhaps India. Closely allied to this genus is *Eurypholis* (fig. 936), of the Lebanon Chalk, which is merely distinguished by the presence of a few dermal scutes. *Cimolichthys*, from the Upper Cretaceous of Europe and the United States, and *Pomognathus* (*Phylactocephalus*), from the Chalk of Europe and the Lebanon, are nearly related genera, mainly distinguished by their dentition. Here also may be placed *Ischyrocephalus*, of the Upper Cretaceous of Westphalia, which may perhaps have had two dorsal fins, and appears to connect *Enchodus* with the *Dercetidæ*.

Family Pachyrhizodontidæ.—Allied to the preceding, but with the body more compressed, and covered with either scutes or scales, or both together, is a group of Fishes which may be provisionally placed in a distinct family. The premaxillæ and maxillæ are large, and carry powerful teeth, which may form one or more rows, and are set in incomplete sockets, and anchylosed to the bone; while the abdominal vertebræ are characterised by their longitudinal striation and the absence of deep pits. The type genus *Pachyrhizodus* (*Hypsodon* in part) ranges in Europe from the Chalk to the London Clay, and also occurs in the Cretaceous of North America; its teeth are so like those of Reptiles that a lower jaw was described as belonging to a species of *Mosasaurus*. *Empo*, of the North American Cretaceous, may be certainly placed in this family; in which we may also probably include *Stratodus*, of the Upper Cretaceous of both Europe and North America. An allied type, from the Lower Miocene of Belgium, has been described under the preoccupied name of *Amphodon*.

Family Saurocephalidæ (Saurodontidæ).—The last family of the Saurodonts are laterally compressed Fishes, in which the maxillæ and premaxillæ are large, and carry powerful teeth, which are usually implanted in distinct sockets. The dentary bone of the mandible has but a single row of similar teeth, and there are no teeth on the palatines and ectopterygoids. The vertebræ, with the exception of those of the cervical region, carry two deep grooves and pits on their lateral surfaces. The type genus *Saurocephalus* is represented in the Cretaceous of North America, and also by a single species in the topmost Cretaceous of Maastricht, in Holland; the teeth are subequal and closely approximated. *Ichthyodectes* and *Portheus* (fig. 937) also occur in the Upper Cretaceous of both Europe and North America; the latter, which extends down to the Gault, attaining large dimensions, and being characterised by the great crest in

the supraoccipital region, by the unequal size of the cylindrical or compressed teeth, and the presence of at least one large spine in the pectoral and pelvic fins. *Ichthyodectes* apparently differs mainly by its equal-sized teeth. Another genus is *Daptinus*, of the North American and English Cretaceous; the English species apparently connecting the typical American one with *Ichthyodectes*. *Saurodon* is known from the Upper Greensand of New Jersey; while we may

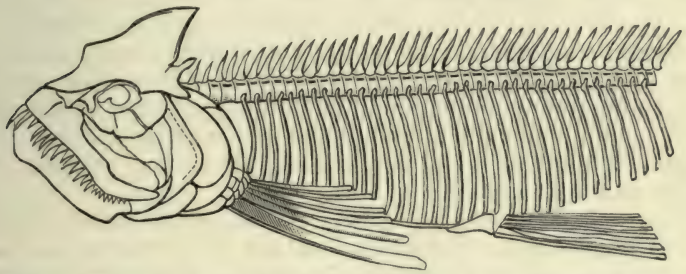

Fig. 937.—The anterior portion of the skeleton of *Portheus molossus*; from the Cretaceous of North America. Greatly reduced. (After Cope.)

provisionally place in this family the imperfectly known *Tomognathus*, of the English Chalk, in which the teeth were anchylosed to the jaws, without sockets, and had subcylindrical crowns enamelled superiorly.

As a probable Saurodont, of which the family position cannot be determined, may be mentioned *Gigantichthys* (*Titanichthys*), founded upon teeth of very large size, from the Cretaceous of Egypt.

Family Gonorhynchidæ.—We may now briefly mention five small existing families related to the Salmonoids and Clupeoids. The first of these is now represented only by a single species of *Gonorhynchus* found on the coasts of South Africa, Australia, and Japan. Closely allied, however, is *Notogoneus*, from the Eocene of Wyoming, which is mainly distinguished by its dentition.

Family Osteoglossidæ.—The second family is now represented by *Osteoglossum* of South Africa, Sumatra, and Queensland; the huge *Arapaima* of the Brazilian rivers; and *Heterotis* of several of those of South Africa; thus presenting a striking example of discontinuous distribution. The only known fossil is *Dapedoglossus*, of the Eocene of Wyoming; a feature in distribution analogous to the occurrence of the genus *Notogoneus* of the preceding family in the same locality.

Family Chirocentridæ.—The genus *Chirocentrus*, of the Indian Ocean, the sole existing member of this family, probably occurs in the Eocene of Sumatra. *Chiromystus*, from the Eocene of Brazil, may perhaps be referable to this family, although it is not certain

that it should not rather be placed in the allied American family *Hyodontidæ*.

Family Esocidæ.—The *Esocidæ* are now represented by the Pikes (*Esox*) of the rivers of the Northern Hemisphere. They are characterised by the margins of the upper jaws being formed by the premaxillæ and maxillæ; by the presence of small conical teeth on the palate; and the absence of an adipose fin, and the position of the dorsal in the hinder part of the body. Species of *Esox* occur in the Upper Miocene of Œningen in Switzerland, and the Pleistocene of Silesia; while the extinct *Sphenolepis*, of the Upper Eocene of Paris and the Eocene of Aix in Provence, characterised by its wedge-shaped scales, is considered to be allied. Recent writers also place in this family the marine *Istiæus* of the Chalk of Westphalia and the Lebanon, in which there is a long dorsal fin occupying the greater part of the back.

Family Scombresocidæ.—The members of this family mainly inhabit tropical and temperate seas, and are best known by the Garpike (*Belone*) and the Flying-fish (*Exocœtus*). The jaws are formed as in the last family; the dorsal fin is placed above the anal in the caudal region, and there is no adipose fin. *Belone* is found in the Miocene of Licata, in Sicily; while *Holosteus* of the Middle Eocene of Monte Bolca is an allied genus. The living genus *Exocœtus* is characterised by the enormous development of the pectoral fins, and was preceded in the Chalk of the Lebanon by the nearly related *Exocœtoides*.

Family Cyprinodontidæ.—The Cyprinodonts are mostly small, carp-like fishes, inhabiting the fresh, brackish, or salt waters of a considerable part of the world; and readily characterised by the presence of scales on the head, and the absence of barbels. Species of the type genus *Cyprinodon* (*Lebias*) occur in the Middle and Lower Miocene of the Continent, while the Œningen beds have yielded a species referred to the South American genus *Pœcilia*. A comparatively large Cyprinodont has been described from the Pliocene of India.

Family Cyprinidæ. — The important family of Carps is very numerously represented in the freshwaters of the Old World and North America. There are no scales on the head; the margin of the upper jaw is formed by the premaxillæ; there are no teeth in the jaws; there is no adipose fin; the lower pharyngeal bones carry one or more rows of teeth; and the mouth frequently has barbels. The body is more or less compressed, and is often comparatively deep. In the Miocene of the Continent we have representatives of the following genera now living in Europe—viz., *Cyprinus* (Carp), *Gobio* (Gudgeon), *Leuciscus* (Roach and Dace), *Tinca* (Tench), *Rhodeus*, which is mainly Asiatic, *Aspius*, and *Cobitis*. *Acanthopsis*,

now confined to India, is represented in the Miocene of Œningen and Puy-de-Dôme; the Oriental genera *Amblypharyngodon* and *Thynichthys* occur in the Eocene of Sumatra, while the names *Cyclurus*, *Hexapsephus*, and *Mylocyprinus* have been applied to North American Tertiary forms, which are probably more or less closely related to those now inhabiting the same region.

Family Scopelidæ.—The Scopeloids are marine fishes allied to the Carps (with which they agree in the structure of the jaws), in which the body may be naked, and there are neither barbels nor swim-bladder. They are represented in past epochs by *Hemisaurida*, of the Cretaceous of Istria, which is allied to the living *Saurus*, and *Parascopelus* and *Anapterus* from the Miocene of Sicily, of which the latter is related to *Paralepis* now found in the same region.

Family Siluridæ.—The Siluroids or Cat-fishes form a large family of freshwater fishes of not less importance than the Carps, inhabiting all temperate and tropical regions, and in some cases entering the sea. The skin is either naked or covered with bony scutes; there are always barbels, which frequently have a bony axis; the margin of the upper jaw is formed by the premaxillæ; there is no subopercular; and there may or may not be an adipose fin. The skull of the Siluroids is often remarkable for the great development of the supraoccipital (fig. 938), and the presence of dermal ossifications in the region of the neck, which spread over the nape, and articulate with the bones of the secondary pectoral girdle. The first and second interspinous bones of the neck frequently also develop a large bony buckler, behind which the long dorsal spine articulates by means of a ring with the first interspinal; and this spine can be fixed in an upright position by a curious mechanism connected with the second interspinal. The "helmet" of the nape may be continuous with the "buckler," and these bones, together with those of the cranium proper, are frequently ornamented with a granular sculpture. The pectoral fins frequently carry a spine as large as that of the dorsal. The pharyngeal teeth are generally knob-like.

From many points in which the Siluroids resemble the Placodermatous Ganoids, Professor Huxley has suggested that we may regard the latter as nearly related to the ancestors of the existing family. Siluroids are not definitely known before the Tertiary, although it has been suggested that *Telepholis*, from the Upper Cretaceous of Westphalia, may belong to this family. In Europe the earliest undoubted member of the family is known by an imperfect skull from the London Clay, which has received the name of *Bucklandium;* the affinities of this form are imperfectly known, but the skull seems to approximate to that of *Auchenoglanis* of the African rivers. In the Middle Eocene of Bracklesham, and the Upper

Eocene of Barton, we have Siluroids referred to the existing tropical genus *Arius;* the peculiar, somewhat heart-shaped, otoliths of these fishes being not uncommon in the Barton beds. It is interesting to notice the association in the English Eocene of Siluroids with Crocodiles and Trionychoid Chelonians; the three groups being found together at the present day in India and Africa. The Eocene of Sumatra has yielded remains of extinct species of the living Oriental genera *Pseudotropius* and *Bagarius;* the last-named genus being also represented in the Pliocene Siwaliks of India by the gigantic *B. Yarrelli*, now inhabiting the Ganges. The same beds have also yielded remains of *Clarias*, now found in both the Oriental and Ethiopian regions, of a species belonging to the genus *Heterobranchus* (fig. 938), which is now confined to the Nile, and not improbably also of *Chrysichthys* of tropical Africa. The existing *Macrones aor* of the Indian and Burmese rivers has also left its remains in the Siwaliks; while the characteristic Oriental genus *Rita* is likewise represented in the same deposits. Finally, of the widely-distributed genus *Arius*, which we have already mentioned from the English Eocene, there is evidence of two Siwalik species; one being apparently nearly allied to a large existing West African form. In the Eocene of North America there occurs the genus *Rhineastes*, which has vomerine teeth, and may be allied either to *Arius* or to *Pimelodus*, while spines from the same deposits have been referred to the latter genus.

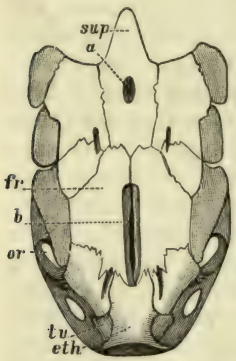

Fig. 938.—Upper view of the skull of *Heterobranchus intermedius;* from the Nile. One-half natural size. *a*, Supraoccipital, and *b*, Frontal vacuities; *eth*, Ethmoid; *fr*, Frontal; *or*, Orbit; *sup*, Supraoccipital; *tu*, Turbinal. The sculpture is omitted.

Family Muræniдæ.—The last family that we have to notice in this suborder is that of the Eels. In these fishes the body is greatly elongated, and either naked, or covered with rudimental scales; the toothed maxillæ form part of the border of the upper jaw, and there are no pelvic fins. Of the freshwater forms, *Anguilla* (Eel) ranges from the present date to the Chalk of the Lebanon, and is abundantly represented in the Miocene of Œningen and the Middle Eocene of Monte Bolca. The Marine forms, or Congers, are represented by species of the existing genus *Ophichthys* in the Monte Bolca beds; and by the extinct *Sphagebranchus* of the latter deposits, and *Rhynchorhinus* of the London Clay. Peculiar larval forms of the type known as *Leptocephali* occur in the Continental Tertiaries, some of which are probably referable to this family.

Suborder 2. Anacanthini.—In this and the four following suborders, together forming the Physoclysti of some writers, the swim-bladder (when present) has no connection with the pharynx, and the pelvic fins are nearly always thoracic or jugular in position—in the latter case being in advance of the pectorals. The present suborder is further characterised by the rays of the dorsal fin being soft and jointed, and the pelvic fin never abdominal.

Family Gadidæ.—In the Cod family the body (fig. 939) is symmetrical, and covered with small scales; there may be three dorsal

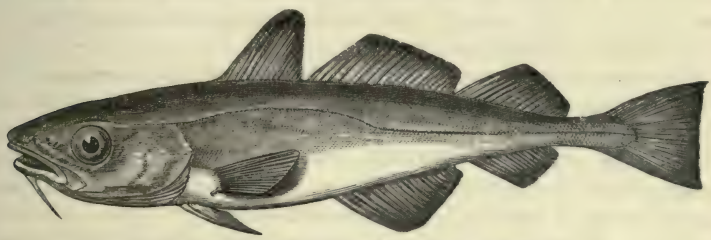

Fig. 939.—The Cod (*Gadus morrhua*). Reduced.

fins, and the pelvic fins are jugular. All the genera are marine, and the family is unknown before the Eocene. The extinct *Nemopteryx* and *Palæogadus* have been described from the Eocene of Glarus; while in the London Clay of Sheppey we have species

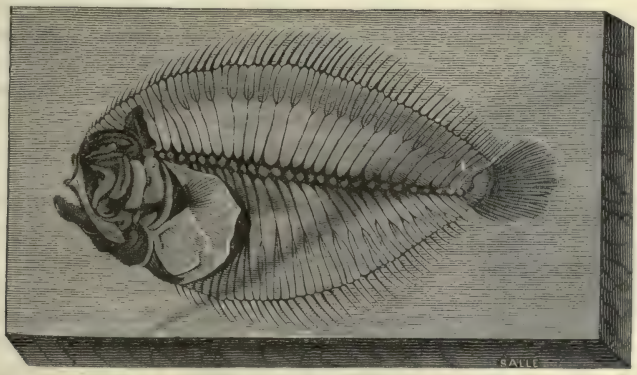

Fig. 940.—Skeleton of *Rhombus minimus*; from the Middle Eocene of Monte Bolca.

allied to *Gadus* (Cod), *Merluccius* (Hake), and *Physis*. Other Gadoids occur in the Miocene of Sicily.

Family Pleuronectidæ.—The Flat-fishes are characterised by the extreme lateral compression of the body (fig. 940), of which the

fore part and the head are not bilaterally symmetrical. They swim with one side upwards and the other downward, the head being twisted round so as to bring the two eyes upon that side which becomes the upper one, and which alone is coloured. There is no swim-bladder, and the dorsal and anal fins occupy almost the entire length of the body. Remains of a species of *Rhombus* or Turbot (fig. 940) are found in the Middle Eocene of Monte Bolca, and those of a *Solea* (Sole) in the Miocene of Würtemberg.

Suborder 3. Pharyngognathi. — In this small suborder a portion of the rays of the dorsal, anal, and pelvic fins is formed by non-articulated spines. The lower pharyngeal bones are united; and the swim-bladder has no duct.

Family Pomacentridæ.—Of this large family the only European fossil representative is *Odonteus* from the Middle Eocene of Monte Bolca, which is allied to the existing *Heliastes;* but Professor Cope thinks that *Priscacara* from the Eocene of North America may perhaps be referable to it, although vomerine teeth are present. All the members of this family have ctenoid scales.

Family Labridæ.—The Wrasses are a large family of littoral fishes most abundant in tropical and temperate regions, and characterised by their cycloid scales, the single dorsal fin, the thoracic position of the pelvic fins, and the absence of teeth on the palate. Many of them have the lips greatly thickened; and the pharyngeal bones bear molariform teeth. The existing genus *Labrus* is recorded from the Middle Eocene of Monte Bolca and the Miocene of Switzerland; while *Saurinichthys* of the Miocene of France appears allied to the living *Odacina*. *Protautaga* of the Eocene of North America is the ancestral form of the Black-fish (*Tautaga*) of the same country.

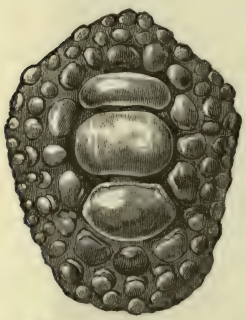

Fig. 941.—Pharyngeal teeth of *Phyllodus* from the London Clay.

Family Pharyngodopilidæ.—A number of extinct fishes more or less nearly allied to the Wrasses, but differing in several points very markedly from that family are regarded as forming a group by themselves. The type genus *Pharyngodopilus* (*Nummopalatus*) occurs in the French Miocene, and in the Tertiary of the Canaries; closely allied to which is *Phyllodus* from the Cretaceous of Germany and the London Clay of Sheppey, derived teeth being also found in the Suffolk Crag. The pharyngeal teeth of *Phyllodus* (fig. 941) are remarkable for their thin and leaf-like structure, and also for the rapid manner in which they are succeeded from below by fresh ones. The imperfectly known *Egertonia* from the Lower Eocene

of Sheppey, and *Platylæmus* from the Middle Eocene of Bracklesham, may be provisionally included in this family.

Family Chromidæ.—The Chromids are a family of small freshwater Fishes from Palestine, tropical Africa, and America; and also represented by one genus in India. The scales are usually ctenoid, the lateral line is interrupted, and the teeth of the jaws are very small. To this family is referred the large genus *Pycnosterinx* from the Cretaceous of the Lebanon; and with less certainty *Imogaster* of the same deposits.

Suborder 4. Acanthopterygii.—The Acanthopterygii form a very large series characterised by part of the rays of the dorsal, anal, and pelvic fins being non-articulated and forming strong spines. The lower pharyngeal bones are usually separate; and there is no duct to the swim-bladder. The scales are very generally ctenoid.

Family Ophiocephalidæ.—The *Ophiocephalidæ* are freshwater fishes, almost confined to the Oriental region, in which the long head and body are entirely covered with scales, and the dorsal and anal fins are long and devoid of spines. These fishes are in the habit of burying themselves in the mud during droughts. The type genus *Ophiocephalus* is represented in the Pliocene of India by species closely allied to, if not identical with some of those now inhabiting the same area.

Families Fistulariidæ and Centriscidæ.—The first of these families comprises the marine "Flute-mouths," characterised by the long body and the production of the anterior bones of the skull into a long tube, terminating in the mouth, and by the absence or small size of the scales. The existing genera *Fistularia* and *Aulostoma*, now found on the borders of the tropical Atlantic and Indian Oceans, are represented in the Eocene of Monte Bolca and Glarus; while *Auliscops*, now confined to the Pacific coast of North America, is found in the Eocene of Sumatra. Extinct genera from Monte Bolca are *Urosphen* and *Rhamphosus*—the former characterised by the wedge-like caudal fin, and the latter by a large spiny ray on the neck. A Fistularian, from the Lebanon Cretaceous, has been named *Solenognathus*, but the name is preoccupied. The *Centriscidæ*, which agree with the *Fistulariidæ* in the structure of the mouth, but differ in the form of the body, are known in a fossil state by a species of the living genus *Amphisile*, from Monte Bolca.

Family Mugilidæ.—This and the two next families include fishes characterised by the presence of two distinct dorsal fins, of which the first is either low, or has weak spines; and by the abdominal position of the pelvic fins, which have five rays and one spine. The Grey Mullets inhabit the coasts of tropical and temperate seas, and have cycloid scales with no lateral line. The recent genus *Mugil* occurs in the Upper Eocene of Aix; and *Calamo-*

pleurus, of the European Chalk, with which the North American genus *Syllæmus* is probably identical, may be placed in this family.

Family Atherinidæ.—These fishes, which differ from the Mullets by the presence of an indistinct lateral line and the great number of the vertebræ, are represented in the Middle Eocene of Monte Bolca by two minute species of the existing genus *Atherina*, and also by the extinct *Mesogaster*.

Family Sphyrænidæ.—The Barracudas, in which the lateral line is continuous and the vertebræ are not numerous, are known at the present day only by *Sphyræna*, of which some species attain a length of eight feet. That genus occurs in the Middle Eocene of Monte Bolca, and has also been recorded from the Upper Cretaceous of the Lebanon; but it is probable that the latter form belongs to one of the Saurodont Physostomi. *Cladocyclus*, from the Upper Cretaceous of England and Brazil, is an extinct genus.

Family Blenniidæ.—The Blennies form one of four families of but little palæontological importance, in which there is a long dorsal fin, which may be entirely spinous; and the ventrals, if present, are either thoracic or jugular. It is probable that *Pterygocephalus*, from the Middle Eocene of Monte Bolca, should be referred to this family.

Family Gobiidæ.—The Gobies belong to another group of the suborder comprising two families, into the characters of which it will not be necessary to enter. They are represented in a fossil state by the existing genus *Gobius*, from the Monte Bolca Eocene, and the extinct *Chirothrix*, from the Upper Cretaceous of the Lebanon.

Family Dactylopteridæ (*Cataphracti*).—This and the next six families form a group of considerably more interest to the palæontologist than the preceding. They are collectively known as the Cottoscombriform section, and are characterised by the presence of spines in at least one of the fins; by the dorsal fins being either continuous or close together; by the spinous dorsal, when present, being short; and when the latter is absent by the length of the soft dorsal. The pelvic fins are always jugal or thoracic. In the present family the body is cylindrical and elongate, with a coat of bony scutes; the dentition is weak; and the pelvic fins are thoracic. *Petalopteryx*, from the Middle Eocene of Monte Bolca, is considered to be related to the existing *Dactylopterus*, in which the pectorals are lengthened to an enormous extent.

Family Cottidæ.—This family is best known by the freshwater Bull-heads (*Cottus*) and the marine Gurnards (*Trigla*). The body is more or less oblong; the dentition weak; the dorsal fin is usually divided, with the soft portion the larger; and the pelvic fins are

thoracic, and generally have five soft rays. *Cottus* itself occurs in the Upper Miocene of Œningen; while the Upper Eocene of Aix yields the extinct *Lepidocottus*, distinguished by its ctenoid scales. *Trigla* occurs in the European Tertiaries.

Family Trachinidæ.—This family comprises a number of genera of small marine Fishes distributed over the greater part of the world, in which the body is long and slender, and may or may not have scales. The dorsal fin may be either single or divided, but its soft portion is always much longer than the spinous. To this family may probably be referred the naked *Callipteryx*, from the Middle Eocene of Monte Bolca; while *Trachinopsis*, of the Upper Tertiary of Spain, is considered to be allied to the existing *Trachinus*—a third extinct genus being *Pseudoeliginus*, of the Sicilian Miocene.

Family Scombridæ.—The *Scombridæ*, typically represented by the Mackerels (*Scomber*), but also comprising other pelagic Fishes, are characterised by the oblong and scarcely compressed body, the well-developed dentition, the two dorsal fins, the general presence of finlets in the posterior part of the body, and the thoracic position of the pelvic fins, which have one spine and five rays. In the Miocene and Eocene of Europe, we meet with species of the existing genera *Scomber* (Mackerel), *Thynnus* (Tunny), and *Cybium*, one Lower Miocene species of the latter having been described under the name of *Scomberodon*. Curiously enough, the specialised genus *Echeneis* (Sucking-fishes) is found in the Lower Eocene of Glarus. *Dictyodus* (*Sphyrænodus*) is an extinct genus from the Lower Eocene of England and the Lower Miocene of Belgium, characterised by the strong development of its dentition, and its single row of conical palatine teeth. Other extinct genera are *Palimphyes* and *Isurus*, of the Lower Eocene of Glarus, and *Orcynus*, from the Middle Eocene of Monte Bolca. The existing *Pelamys* has been recorded from the Lower Miocene of Belgium.

Family Coryphænidæ.—Another pelagic family allied to the preceding is represented by the well-known Coryphænas, popularly known by the misnomer of Dolphins. The body is compressed; the teeth, if present, are small and conical; and there is a long undivided dorsal fin, without a distinct spinous portion. The existing genus *Mene* (*Gastrocnemus*) is found in the Middle Eocene of Monte Bolca; while the family is also represented by the extinct *Goniognathus*, of the London Clay.

Family Cyttidæ.—The Dories have the body very deep and much compressed, with the dorsal fin divided, and its spinous portion taller than the soft part, and the pelvic fins thoracic. They are represented by a species of the existing genus *Zeus*, in the Miocene of Sicily, and also by the extinct *Cyttoides*, of the Lower Eocene of Glarus.

Family Carangidæ.—Of great interest to the palæontologist are the so-called Horse-Mackerels, on account of the beautiful preservation of some of the fossil forms in the Middle Eocene of Monte Bolca. The body is more or less compressed, and may be oblong or deep, and either with or without scales. The dorsal fin, which

Fig. 942.—*Semiophorus velicans*; from the Middle Eocene of Monte Bolca. A, Anal; C, Caudal; D, Dorsal; P, Pectoral; V, Pelvic fins.

may be single or divided, has the spinous smaller than the soft part; and the pelvic fins, if present, are thoracic. One of the most remarkable extinct genera is *Semiophorus* (fig. 942), in which the dorsal fin is of enormous height, while the pelvic fins are also greatly produced. This genus is known only from the Monte Bolca Eocene. Other extinct Tertiary genera are *Pseudovomer*,

from the Miocene of Sicily; *Amphistium* and *Ductor*, from Monte Bolca; *Archæus* and *Plionemus*, from the Lower Eocene of Glarus; and *Æpichthys* and *Vomer*, from the Chalk of Istria. Among existing genera, *Platax* (fig. 943), popularly known as Sea-Bats, from the great height of the fins, occurs in the Red Crag, in the Monte

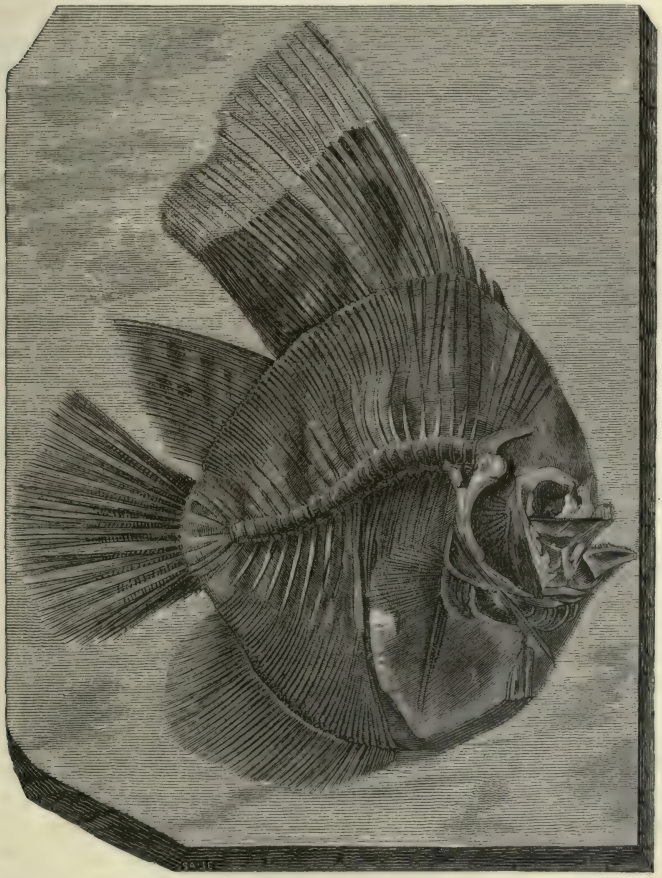

Fig 943.—*Platax altissimus*; from the Middle Eocene of Monte Bolca. Reduced.

Bolca Middle Eocene, and in the Chalk of the Lebanon and England. The dorsal fin is single, and the spinous portion is nearly entirely concealed, consisting only of from three to seven low spines; the jaws are remarkable for their excessive shortness. Other living genera found in the Monte Bolca beds are *Zanclus*,

Caranx (*Carangopsis*), *Argyriosus* (*Vomer*), *Lichia*, and *Trachynotus*; and *Equula*, from the Miocene of Sicily.

Family Acronuridæ.—The last family of the Cottoscombriform section comprises tropical marine Fishes, popularly known as Surgeons, which are readily recognised by the sharp spine bordering each side of the tail. The body is compressed, and oblong or ovate, with small scales; the front of the jaws has chisel-like or pointed teeth; and the dorsal fin is undivided, with the spinous portion less than the soft. This family is represented in a fossil state by species of the existing genera *Naseus* and *Acanthurus* from the Middle Eocene of Monte Bolca.

Family Trichiuridæ. — The next section of the suborder is represented by the existing Scabbard-fishes and the extinct *Palæorhynchidæ*. These Fishes are characterised by their elongated, compressed, or band-like bodies, furnished with long dorsal and anal fins, of which the former may be divided into a number of finlets, somewhat after the manner of the Ganoid genus *Polypterus*. All these fishes are marine, and are found in tropical and subtropical seas. Species of the existing genus *Lepidopus* (Scabbard-fish) occur in the Miocene of Sicily, while *Hemithyrsites* and *Trichiurichthys*, of the same deposits, are forms allied to the living *Thyrsites* and *Trichiurus*, but differing by having the body scaled. *Xiphopteryx* is another extinct genus from the European Eocene; while *Anenchylum*, of the Lower Eocene of Glarus, resembles *Lepidopus* except for the presence of some long rays in the pelvic fins, and the two are probably identical.

Family Palæorhynchidæ.—The members of this family differ from the last by the production of the jaws into a long rostrum, which is either edentulous or provided with very small teeth. The dorsal fin occupies the whole length of the body, and the anal is also elongated and reaches nearly to the forked caudal. This family is known only by *Hemirhynchus* from the Eocene of the Paris basin, and *Palæorhynchus* from the Lower Eocene of Glarus.

Family Xiphiidæ.—The Sword-fishes, which are of pelagic habits, and generally attain very large dimensions, are characterised by the production of the upper jaw into a long spear-like rostrum. They are represented at the present day by *Xiphias* (fig. 944), in which pelvic fins are wanting; and *Histiophorus*, in which these organs are long and filiform, and the dorsal fin may be of great length and height. Fossil Sword-fishes from the London Clay have been referred to *Histiophorus* (*Tetrapturus*), although it is not certain that they may not prove generically distinct. The genus *Cælorhynchus*, which was formerly referred to this family, is noticed among the Chimeroidei.

Family Berycidæ.—The *Berycidæ* are characterised by the pres-

ence of mucous-bearing cavities in the head, and by the pelvic fins having (except in *Monocentris*) a single spine, and more than five rays. This family is one of the oldest of the suborder, being abundantly represented in the Chalk. The fossil genera, which may be noticed in alphabetical order, are as follows—viz., *Acrogaster*, from the Upper Cretaceous of Westphalia; *Berycopsis*, from the Creta-

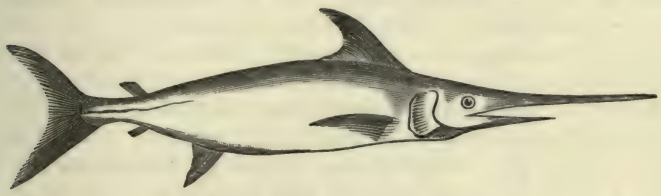

Fig. 944.—*Xiphias*. Greatly reduced.

ceous of England; *Beryx*, in which there is one dorsal fin with several spines, is represented by a single species in the European Chalk, and by two species in the Chalk of the Lebanon, while it is also living at the present day; *Holocentrum*, from the Middle Eocene of Monte Bolca, the Miocene of Malta, and tropical seas of the present day; *Homonotus*, from the Cretaceous of both England and the Lebanon; *Hoplopteryx* (fig. 945), in which the spinous portion of the dorsal fin is greatly developed, and there are also four

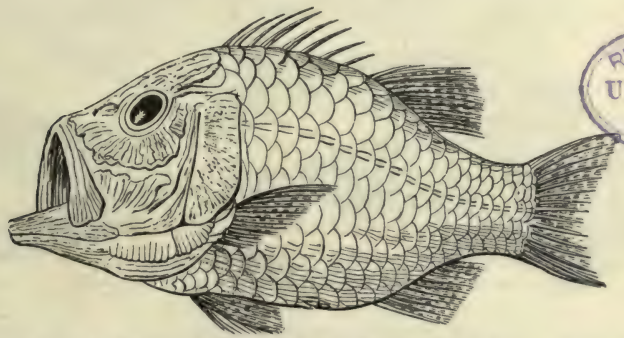

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Fig. 945.—*Hoplopteryx lewesiensis*; from the Upper Chalk of Sussex. Reduced. (After Mantell.)

large spines in advance of the anal, is known from the Upper Cretaceous of both Europe and the Lebanon; *Myripristis*, from the Middle Eocene of Monte Bolca, and now found in tropical seas; *Pristigenys*, from Monte Bolca; *Pseudoberyx*, from the Chalk of the Lebanon, characterised by the almost abdominal position of the pelvic fins; *Sphenocephalus*, from the Upper Cretaceous of West-

phalia; and *Stenostoma*, from the English Chalk, of which the affinity is somewhat doubtful.

Perciform Section.—The remaining families of this suborder are characterised by their more or less compressed body; by the dorsal fin, or fins, occupying the greater portion of the back; by the strong development of the spinous part of the dorsal fin, which is at least as long as the soft portion; and by the soft anal corresponding to the soft dorsal. The pelvic fins are thoracic.

Family Scorpænidæ.—This family, which is allied to the following, but has villiform teeth, is known in a fossil state only by a species of the type genus *Scorpæna*, from the Eocene of Algeria.

Family Sparidæ. — The Sea-Breams resemble the Percoids, which we shall notice immediately, in general appearance, but the mouth is either provided in front with chisel-like teeth, or on the sides with molariform ones. All of them inhabit tropical and temperate seas. Among existing genera the sphæroidal palatal teeth of *Chrysophrys* occur in the Red Crag of Suffolk, the Miocene of Malta, and in beds in the Canaries, which are probably referable to the same epoch; while *Sargus* is recorded from the Miocene of France and Würtemberg, the Upper Eocene of Algeria, and the older Tertiary of New Zealand; and *Pagellus* occurs in the Chalk of the Lebanon. It appears, moreover, that many of the crushing palatal teeth of *Chrysophrys* have been described as *Sphærodus*, while the anterior cutting-teeth of the same genus, together with pharyngeal teeth of some of the Carps, have been described as *Capitodus*.

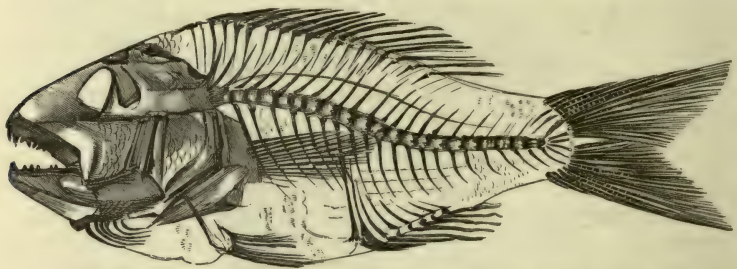


Fig. 946.—Skeleton of *Sparnodus micracanthus*; from the Middle Eocene of Monte Bolca. Reduced

Cutting-teeth of this type, described under the latter name, occur in the Miocene of Austria and Silesia, the Pliocene of Italy, and the Eocene of Northern India. *Sparnodus* (fig. 946) is an extinct genus from the Middle Eocene of Monte Bolca, while the name *Stephanodus* has been applied to a genus from the Upper Chalk of the Sahara, characterised by the breadth and denticulated edges of the cutting-teeth. It may also be observed that teeth from the European

Tertiaries have been described under the names of *Sargodon*, *Soricidens*, and *Asima*.

Family Chætodontidæ. — The Coral-fishes, or Chætodonts, differ from the Percoids in the greater vertical depth of the body, by the continuation of the scales over the median fins, and also by the lateral line stopping short of the caudal fin. Their teeth are bristle-like. These marine tropical fishes (which are generally described under the name of *Squamipennes*) are remarkable for the extreme gorgeousness of their colouring, and are of comparatively small size. They are represented in the Middle Eocene of Monte Bolca by the existing genera *Holacanthus*, *Pomacanthus*, *Ephippus*, *Scatophagus*, and *Toxotes;* the latter being now confined to the Oriental and Australian regions. The earliest Chætodont is *Platycormus*, of the Upper Cretaceous of Westphalia.

Family Percidæ.—With this and the next family of highly specialised Fishes we come to the end of the existing representatives of the present suborder. These Fishes are characterised by the continuous lateral line (fig. 947), the general absence of scales from the median fins, the conical teeth, and the absence of barbels. They are all carnivorous, and inhabit the freshwaters and coasts of

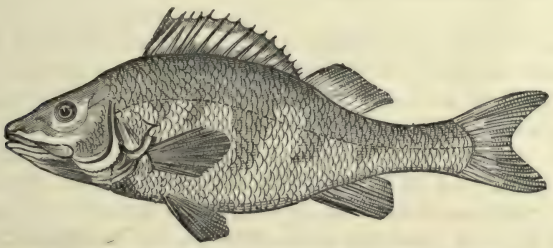


Fig. 947.—The Common Perch (*Perca fluviatilis*). Reduced.

all tropical and temperate regions. The existing genus *Perca* (Perch) occurs in the Upper Miocene of Œningen; while in the Upper Eocene of Aix we have the allied but extinct *Paraperca*. In the Middle Eocene of Monte Bolca, we find species referable to the existing genera *Labrax* (Bass); *Lates*, now inhabiting the Nile and Ganges; *Dules*, of the Indo-Pacific; *Serranus* (Sea-Perch); *Apogon*, of the Mediterranean and Atlantic; and also *Therapon*, of the Indo-Pacific. The extinct *Cyclopoma* and *Smerdis* (fig. 948) likewise occur in the same deposits; the latter being also found at Aix and in the Miocene of Würtemberg. *Acanus* and *Podocys*, from the Lower Eocene of Glarus, are members of this family, which were formerly referred to the *Berycidæ*. In the Eocene of North America we have *Mioplosus*, presenting characters common to

Perca and *Labrax;* and also *Plioparchus*, which does not appear allied to any existing genus.

Family Pristipomatidæ.—This family includes the existing *Pristipoma*, which Dr Günther refers to the *Percidæ*. It occurs fossil in the Eocene of Monte Bolca; and Dr von Zittel would place *Sciænurus*, of the London Clay, in the same family.

Families Aphrodediridæ and Asineopidæ.—These two families are proposed by Professor Cope for the reception of certain North American Eocene Fishes more or less closely allied to the Percoids. The first family includes the genus *Aphrodedirus*, *Erismatopterus*, and *Amphiplaga*, and the second *Asineops*. Professor Cope suggests that *Pygæus*, from the Middle Eocene of Monte Bolca, should perhaps be included in the *Asineopidæ*.

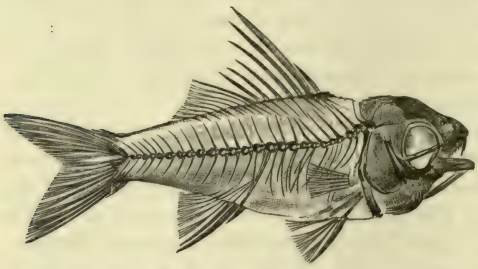


Fig. 948.—Skeleton of *Smerdis minuta;* from the Upper Eocene of Aix, Provence.

Suborder 5. Lophobranchii. — In this small, and to the palæontologist unimportant, suborder the gills are reduced to small round lobes; the gill-cover has only one large plate; and there is a dermal bony skeleton taking the place of the soft integuments. The swim-bladder has no duct.

Family Solenostomatidæ.—The skull is produced into a long rostrum, terminated by the toothless mouth. The gill-openings are wide; there are two dorsal fins; and all the others are well developed. The only existing genus is *Solenostoma*, allied to which is *Solenorhynchus*, of the Italian Eocene.

Family Syngnathidæ.—The Sea-horses and Pipe-fishes differ from the preceding family by the small gill-opening, the single dorsal fin, and the absence of the pelvic fins. The first section, in which the tail is not prehensile, includes the Pipe-fishes, and is represented in the Miocene of Italy and the Middle Eocene of Monte Bolca by the existing genera *Syngnathus* and *Siphonostoma*, and also by the extinct *Calamostoma*, which is allied to *Hippocampus*, but has a caudal fin. The Sea-horses do not appear to be represented in a fossil state.

Suborder 6. Plectognathi.—The last suborder is likewise of small extent, and is characterised as follows. The skin may be naked, or covered with rough scales, scutes, or spines, and the skeleton is imperfectly ossified. There is a small opening leading to the pectinate gills in advance of the pectoral fin; the bones of

the upper jaw are generally welded together; there is a soft dorsal fin; but the pelvic fins are either in the form of spines or absent. There is no duct to the swim-bladder.

Family Balistidæ.—The File-fishes and Coffer-fishes, which are frequently known as *Sclerodermi*, have the jaws somewhat produced, and armed with a small number of teeth; the skin being covered either with rough scales or scutes, and traces of pelvic and spinous dorsal fins always remaining. *Balistes* (File-fish) is characterised by its chisel-like teeth, admirably suited for browsing on the corals on which these fishes subsist. *Protobalistum*, of the Middle Eocene of Monte Bolca, is supposed to be an ancestral type of *Balistes;* while *Protacanthodes*, of the same deposits, is an allied, but distinct form. The Lower Eocene of Glarus has yielded the extinct *Acanthoderma* and *Acanthopleurus*, which are likewise regarded as allied types; while *Glyptocephalus*, of the London Clay, differs from *Balistes* by the regular rows of tubercles with which the body is covered. *Ostracion* (Coffer-fish), in which the body is invested by a carapace of hexagonal scutes articulating by their edges, is now abundant in subtropical and tropical seas, and appears for the first time in the Middle Eocene of Monte Bolca.

Family Diodontidæ.—In the Globe- and Sun-fishes (the *Gymnodontes* of many writers) the body is more or less shortened; the bones of the jaws are united into a trenchant beak, with or without a median suture; and there are no spinous dorsal, or pelvic fins. The dentition is in the form of laminated dental plates. Among the Globe-fishes, in *Tetrodon*, of which no fossil forms have been described, the dental plates are trenchant, and confined to the margins of the jaws. In *Diodon*, however, in addition to these alveolar plates, there is a median crushing-plate (fig. 949), traversed by a suture, developed on the palate of each jaw. The obliquity of the component laminæ of these plates causing an admirable triturating surface. Fossil palatal plates of this genus are found in the Miocene of Malta and Sicily, in the Middle Eocene of Monte Bolca, and also in the Eocene of Algeria and the Arakan coast. The extinct *Enneodon* is an apparently allied genus from the Italian Tertiary. Finally, the huge pelagic Sun-fishes of the genus *Orthagoriscus*, in which the body is compressed and very short, the vertical fins are confluent, and the tail truncate, occur in a fossil state in the Lower Miocene or Upper Eocene of Belgium. The alleged occurrence of this genus in the English Chalk is, however, based on a misinterpretation.

Fig. 949. — Posterior dental plate of *Diodon Scillæ;* from the Miocene of Malta.

At the conclusion of this order we may mention the genus

Ancistrodon, founded upon detached teeth from the Chalk of France; similar teeth also occurring in the Cretaceous of Texas. These teeth are generally regarded as pharyngeal teeth of Teleostei, although it has been suggested that they may prove to be anterior teeth of Pycnodont Ganoids.

LITERATURE OF PISCES.

1. AGASSIZ (L.)—"Recherches sur les Poissons Fossiles." Neuchâtel. 1833-44.
2. —— "Monographie des Poissons fossiles du Vieux Grès Rouge." Neuchâtel. 1844.
3. COPE (E. D.)—"The Vertebrata of the Cretaceous Formations of the West." 'Rep. U.S. Geol. Survey of the Territories,' vol. ii. (1875).
4. DAVIS (J. W.)—"On the Fossil Fishes of the Carboniferous Limestone Series of Great Britain." 'Trans. Roy. Dublin Soc.' (2), vol. i. (1887).
5. —— "The Fossil Fishes of the Chalk of Mount Lebanon in Syria." *Ibid.*, vol. iii. (1887).
6. EGERTON (P. DE M.)—"The Nomenclature of the Fossil Chimæroid Fishes." 'Quart. Journ. Geol. Soc.' vol. iii. (1847).
7. GÜNTHER (A.)—"Description of Ceratodus." 'Phil. Trans.' 1871.
8. —— "An Introduction to the Study of Fishes." Edinburgh. 1880.
9. HANCOCK (A.) AND ATTHEY (J.)—"On Dipterus and Ctenodus." 'Ann. and Mag. Nat. Hist.,' ser. 4, vol. vii. (1871).
10. HASSE (C.)—"Das Naturliche System des Elasmobranchier auf. Grundlage des Baues und der Entwickelung ihrer Wirbelsauler." Jena. 1879.
11. HUXLEY (T. H.)—"Essay upon the Systematic Arrangement of the Fishes of the Devonian Epoch." 'Mem. Geol. Survey of Great Britain.' Decade X. (1861).
12. —— "Structure of Crossopterygian Ganoids." *Ibid.* Decade XII. (1866).
13. —— "Structure of Ceratodus." 'Proc. Zool. Soc.' 1876.
14. KOKEN (E.)—"Ueber *Pleuracanthus*." 'Sitz. Ges. Nat. Berlin. 1889. No. 3.
15. MIALL (C. J.)—"On the Genus *Ceratodus*, with Special Reference to the Fossil Teeth found at Maledi, Central India." 'Palæontologia Indica' (Mem. Geol. Surv. Ind.), ser. 4. vol. i. (1878).
16. —— "Sirenoid and Crossopterygian Ganoids." 'Palæontographical Society.' 1878.
17. NEWBERRY (J.)—"Palæontology of Ohio" (Carboniferous and Devonian Fishes). 1873 and 1875.
18. NEWTON (E. T.)—"The Chimæroid Fishes of the British Cretaceous Rocks." 'Mem. Geol. Survey of Great Britain.' Monograph IV. (1878).
19. OWEN (R.)—"Odontography." London. 1840-45.
20. PANDER (C. H.)—"Die Placodermen." 1857.
21. —— "Die Ctenodipterinen des Devonischen Systems." 1858.
22. —— "Die Saurodipterinen, Dendrodonten, Glyptolepiden, und Cheirolepiden des Devonischen Systems." 1860.

23. PANDER (C. H.)—"Fossilen Fische des Silurischen Systems." 1856.
24. POWRIE (J.) AND LANKESTER (E. R.)—"Monograph of the Fishes of the Old Red Sandstone of Britain (*Cephalaspidæ*)." 'Palæontographical Society.' 1868-70.
25. TRAQUAIR (R. H.)—"Description of *Pygopterus Greenockii*," &c. 'Trans. Roy. Soc. Edinb.,' vol. xxiv. (1867).
26. —— "Monograph of the Ganoid Fishes of the British Carboniferous Formations (*Palæoniscidæ*)." 'Palæontographical Society.' 1877.
27. —— "On the Genus *Dipterus*," &c. 'Ann. and Mag. Nat. Hist.,' ser. 5, vol. ii. (1878).
28. —— "On the Structure and Affinities of *Tristichopterus alatus*." 'Trans. Roy. Soc. Edinb.,' vol. xxvii. (1875).
29. —— "On the Cranial Osteology of *Rhizodopsis*." *Ibid.*, vol. xxx. (1881).
30. —— "Report on Fossil Fishes collected in Eskdale and Liddesdale." Pt. I. Ganoidei. *Ibid.*, vol. xxx. (1881).
31. —— "Structure and Systematic Position of *Cheirolepis*." Also "On Some Fossil Fishes from the Neighbourhood of Edinburgh." 'Ann. and Mag. Nat. Hist.,' ser. 4, vol. xv. (1875).
32. —— "On the Structure and Affinities of the *Platysomidæ*." *Ibid.*, vol. xxix. (1879).
33. —— "On the Nomenclature of the Fishes of the Old Red Sandstone of Great Britain." 'Geol. Mag.,' decad. 3, vol. v. (1888).
34. —— "On the Structure and Classification of the *Asterolepidæ*." 'Ann. Mag. Nat. Hist.,' ser. 6, vol. ii. (1888).
35. —— "*Homosteus* compared with *Coccosteus*." 'Geol. Mag.,' decad. 3, vol. vi. (1889).
36. WHITEAVES (J. F.)—"Illustrations of the Fossil Fishes of the Devonian Rocks of Canada." Pts. I. and II. 'Trans. Roy. Soc. Canada,' vols. iv. and vi. (1887 and 1889).
37. WOODWARD (A. S.)—"On some New Species of *Holocentrum*, from the Miocene of Malta, with a List of Fossil *Berycidæ*." 'Geol. Mag.,' decad. 3, vol. iv. (1887).
38. —— "On Some Remains of the Extinct Selachian *Asteracanthus*, from the Oxford Clay of Peterborough." 'Ann. Mag. Nat. Hist.,' ser. 6. vol. ii. (1888).
39. —— "On the Fossil Fish-spines named *Cœlorhynchus*." *Ibid.*
40. —— "On the genus *Rhacolepis*." 'Proc. Zool. Soc.' 1887.
41. —— "On the genus *Notidanus*." 'Geol. Mag.,' decad. 3, vol. iii. (1886).
42. —— "Synopsis of the Vertebrate Fossils of the English Chalk." 'Proc. Geol. Assoc.,' vol. x. (1887).
43. —— "Catalogue of Fossil Fishes in the British Museum." Pt. I. Elasmobranchei. 8vo, London (1889).
44. —— "On the Occurrence of *Onychodus* in the Lower Old Red of Herefordshire." 'Geol. Mag.,' decad. 3, vol. v. (1888).
45. —— "On the Palæontology of Sturgeons." 'Proc. Geol. Assoc.,' vol. xi. (1889).
46. ZITTEL (K. A.)—"Handbuch der Palæontologie." Abth. I., vol. iii., pts. 1, 2. 8vo, Munich (1887-88). Critically reviewed by A. Smith-Woodward in the 'Geol. Mag.' for 1889.

CHAPTER LI.

CLASS AMPHIBIA.

GENERAL STRUCTURE AND ORDERS.

The Amphibia, which comprise the Frogs and Toads, Salamandroids, Cæcilians, and the extinct Labyrinthodonts, and are sometimes known as the Batrachia, agree in so many points of structure with the more generalised Fishes, that Professor Huxley groups the two classes together under the common name of Ichthyopsida. Recent observations on fossil forms, tend, however, to show in the other direction a transition from the Amphibia to the more generalised Reptilia. The Amphibia as a whole differ from Fishes mainly by the circumstance that when median fins are present they are devoid of fin-rays; and that the limbs, when present, contain the same skeletal elements as those of the higher classes. They agree with Fishes in having branchiæ in their earlier stages of life, but these very frequently disappear in the adult, when respiration is carried on entirely by means of the lungs. An epidermal exoskeleton is generally wanting. There is no amnion, and at best but an imperfect allantois in the embryo. In existing forms the cranium always articulates to the vertebral column by two distinct exoccipital condyles, but in a few Labyrinthodonts these were not ossified. The mandible articulates to the cranium without the intervention of a suspensorium; so that the skull, like that of the Dipnoid Fishes, is autostylic. A large parasphenoid is always present; and cranial bones are largely developed, although their number is generally less than in Fishes. The external nares are terminal in nearly all cases. The vertebral column is more or less completely ossified, and can generally be differentiated into cervical, dorso-lumbar, sacral, and caudal regions; the sacrum but rarely comprising more than a single vertebra. The infraneural segments of the vertebral column are frequently amphicœlous, and in recent forms each bears its own arch; but in certain Labyrinthodonts, as we shall see below, the neural arches are carried by alter-

nate vertebral segments, and from circumstances to be detailed in the sequel it is inferred by Professor Cope and others that the vertebral bodies of existing Amphibians are really intercentra, carrying the neural arches which have been shifted to them from the lost centra. The ribs may articulate to the vertebra by a single (upper) transverse process; but in Salamandroids and Labyrinthodonts the vertebræ also carry an inferior rib-facet, when the heads of the ribs are consequently double. As a rule no ribless (lumbar) vertebræ occur, and sternal ribs are wanting. The sternum, which is never present in Fishes, appears in the Amphibia in the middle line of the chest, and may be extended anteriorly as an omo- and episternum (fig. 974, B). The pectoral and pelvic girdles are well developed; the former (*ibid.*) in recent forms having, however, no clavicle or interclavicle, although it is nearly certain that these bones are represented in the thoracic buckler of the Labyrinthodonts. A distinct rod-like precoracoid (fig. 974, B) occurs in recent forms. In the pelvis the pubis is frequently unossified, and if ossified is much smaller than the ischium. In most cases the ischium and the cartilaginous or bony pubis of either side unite to form a continuous plate, in which the obturator foramen is not represented, although there is a small perforation; and the ischia meet in a ventral symphysis. The body of the ilium may be almost wholly in advance of the acetabulum. The limbs vary greatly in their proportionate length in the different orders, and may be entirely absent; while the carpals and tarsals may be unossified. The limb bones of the Labyrinthodonts approximate to those of the Anomodont Reptiles. The carpus and tarsus always have a centrale, and in some of the primitive Labyrinthodonts there may be at least three centralia in the latter. The fourth and fifth tarsalia always remain distinct from each other in those forms which have five digits. The latter number is found in the Labyrinthodonts, but in some existing forms the digits may be reduced to three or two. The number of the phalangeals in the digits of pentedactylate forms, counting from the first to the fifth, does not exceed 2, 2, 3, 3, 3, and this number may be reduced in some existing forms. As a rule the tail is comparatively short.

Teeth are usually present on the premaxilla, maxilla, vomer, and the dentary bone of the mandible; but are generally wanting on the palatine and pterygoid, although present on the latter, and also on the parasphenoid, in many Labyrinthodonts. These teeth are usually anchylosed to the bone, and in existing forms are of simple structure. In the Labyrinthodonts the structure of the teeth may, however, become very complex by foldings of the dentine, this structure being an extreme development of that met with in certain Ganoids; and in some of these forms the usually large pulp-cavity

may be greatly reduced. In existing forms there is generally no exoskeleton, and if scutes or scales are developed they are buried in the skin; but in the Labyrinthodonts bony scutes were very generally present, although frequently restricted to the ventral aspect of the body.

A marked, although not universal, feature in the class is the change from a respiration by gills to one by lungs; this change being accompanied by other structural alterations, and termed a metamorphosis. In some instances only external gills are developed, which form a plume on either side of the neck; and it is these gills which persist in such forms as do not undergo a metamorphosis. In those groups, however, in which a metamorphosis takes place internal gills may be developed for a short period.

That the Amphibia have taken their origin from primitive Fishes allied to the Dipnoi and Ganoidei is pretty evident. Evidence of

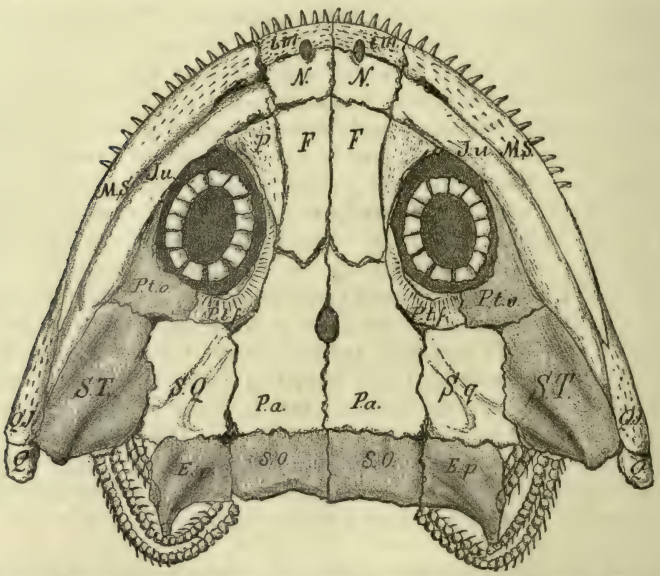


Fig. 950.—Enlarged view of the upper surface of the cranium of *Protriton*, with the characteristic Labyrinthodont bones shaded; from the Permian of Bohemia. *N*, Nasal; *F*, Frontal; *P.a*, Parietal; *S.O*, Supraoccipital; *E.p*, Epiotic; *S.T.*, Supratemporal; *S.q*, Squamosal; *P.t.f*, Postfrontal; *Ju*, Jugal; *P.t.o*, Postorbital; *im*, Premaxilla; *M.S*, Maxilla; *QJ*, Quadratojugal; *Q*, Quadrate. (After Fritsch.)

affinity with the primitive Ganoids is indeed very clearly shown by the so-called labyrinthic structure of the teeth of nearly all the Palæozoic Amphibia, since we find a similar type of dental structure obtaining in many of the early Ganoids, and nowhere else in the

whole animal kingdom. The similarity in the structure of the vertebral column of the earlier Elasmobranch and Ganoid Fishes with that of the Labyrinthodont Amphibians is also important evidence pointing in the same direction.

This class may be divided into the four orders, Labyrinthodontia, Apoda, Ecaudata, and Caudata. The first is totally extinct, the second is at present unknown before the existing epoch, while we have no certain record of the occurrence of the third before the Cretaceous, and of the fourth previously to the Tertiary.

Order I. Labyrinthodontia.—Since the name of this order is not strictly applicable to all its members it has been proposed to substitute the term Stegocephala; but, as the same objection might be taken to a large number of terms in use, such a change seems unnecessary. Using, then, the Labyrinthodontia as including the Ganocephala and Microsauria of some writers, its members may be characterised by the following features. The body is more or less elongated, and furnished with a tail; the skull has paired supraoccipitals (fig. 950, *S.O*), and its postero-lateral regions are roofed over by a postorbital (*P.t.o*) anteriorly, and a supratemporal (*S.T*) posteriorly. There is, moreover, very generally an epiotic [1] (*E.p*); the orbits frequently have a bony ring in the sclerotic; and there is a

Fig. 951.—Ventral aspect of the thoracic buckler of *Actinodon Frossardi*; from the Permian of France; two-fifths natural size. *ent*, Interclavicle; *ep*, Clavicle; *s.cl*, Supraclavicle; *o*, Scapula. (After Gaudry.)

parietal foramen. Palatine and vomerine teeth are very generally present, and the dentine of the teeth is frequently more or less folded, or plicated, from the sides. The centra of the vertebræ, which are amphicœlous, may be imperfectly ossified, and frequently retain a notochordal canal in the middle. Usually there is a buckler on the inferior surface of the thorax, consisting of one median, and two lateral flattened bones, probably representing the interclavicle and clavicles; the relations of these bones being shown in fig. 951.

[1] Dr Baur regards this bone as the opisthotic; and also considers that the bone here termed the squamosal is the supratemporal, and *vice versâ*.

Posteriorly to this thoracic buckler an armour of dermal scutes is generally developed on the ventral surface of the body; and in some cases this armour may cover the entire body, the form of the scutes, or scales, then varying considerably in the different regions. Four paired pentedactylate limbs were usually present.

The pterygoids are always separated from one another in the median line. The pelvis[1] of the more typical forms is remarkably like that of the Pariasaurian Anomodont Reptiles, presenting the same absence of an obturator foramen.

The paired supraoccipital ossifications constitute a feature found elsewhere only among the Ganoid Fishes; and the frequent ossification of the articular bone of the mandible is also a character not found elsewhere in the class. In many cases the external surface of the bones of the skull (fig. 952), and of the thoracic buckler, is

Fig. 952.—Lateral view of the imperfect left ramus of the mandible of *Pachygonia incurvata*; from the Lower Mesozoic of India. The letters indicate mucous canals. (After Huxley.)

sculptured by a series of irregular grooves and ridges; traversed in the former instance by a number of mucous canals. From the occurrence of a similar sculpture in the Pariasaurian Anomodonts and the Crocodilians, Professor Seeley regards these groups as directly descended from Labyrinthodonts; and it is evident that the passage from the Labyrinthodonts to the former group of Reptiles is almost a complete one. The gills (fig. 953) of the young are generally lost in the adult; but in one group the external gills persist.

Labyrinthodonts range in Europe generally from the Carboniferous to the Trias, and are especially abundant in the Permian; but one genus (*Rhinosaurus*) persisted to the Lower Jurassic. In North America and India this order is abundantly represented in strata mainly representing the period from the Carboniferous to the Trias. According to the views of Professor Cope and Dr Fritsch, this order is to be regarded as one presenting generalised characters, some of which approximate to those of modern Amphibia, while others are

[1] It should be observed that in the figure of the pelvis of *Eryops* given in Zittel's 'Palæontologie,' abth. i., vol. iii., pt. ii., p. 364, fig. 351, the hinder end of the ischium is mistaken for the pubis.

Reptilian; and we may probably regard the Anomodont Reptiles as having taken their origin from a group closely allied to the Labyrinthodonts, if not actually from this order. As regards the subdivisions of the order there is still considerable uncertainty, and all such divisions must consequently be regarded as more or less provisional. Dr Fritsch has, indeed, proposed to range the families under four series or suborders, according to the external contour of the body and the nature of the vertebral column; this grouping being provisionally adopted in the present work, with some emendation of nomenclature.

Suborder 1. Branchiosauria.—In this suborder the external appearance approaches that of the modern Salamanders. The vertebræ have centra composed of a single piece, which retains traces of the notochord; the ribs are short and straight; and the neural canal is dilated in the middle of each vertebra. The teeth are simple in structure, and internal gills were developed in the young. Some authorities include the next two groups in the present suborder under the name of Lepospondyli.

Family Protritonidæ.—The *Branchiosauridæ* of Dr Fritsch, being founded on a name which is apparently a synonym, may be better known as the *Protritonidæ*. They are characterised by the great breadth of the skull (fig. 950), and the smooth teeth. Typically the palatines, according to Dr Credner, are small transversely elongated bones lying in the anterior part of the skull, and not joining the maxillæ; this arrangement being similar to that found in the Ecaudata. The type genus *Protriton* (*Branchiosaurus* or *Pleuronura*) is found abundantly in the Permian of the Continent; and its development has been fully worked out by Dr Credner from the study of a large number of specimens of all ages. The specimen shown in fig. 953 exhibits the nearly entire skeleton of a small individual, while the details of the cranial structure are exemplified in the greatly enlarged skull shown in fig. 950.

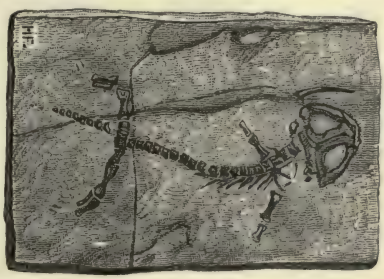


Fig. 953.—Ventral aspect of the nearly entire skeleton of a young individual of *Protriton petrolei*; from the Permian of France. (After Gaudry.)

According to the observations of Dr H. Credner, it appears that the youngest specimens known were 25 mm. in length, in which stage the creature was aquatic, and breathed by gills, which were supported by four pairs of arches. By the time they attained a length of from 60

to 70 mm., these larvæ cast their gills, and became air-breathers; their development being thus analogous to that of the existing Salamanders. The adults measure from 100 to 160 mm. In the course of the metamorphosis the skull decreases somewhat in width, and the thoracic buckler grows much more rapidly than the scapula and coracoid, while, curiously enough, the pelvis shifts its position, and thus increases the number of presacral vertebræ from 20 to 26. In the larva the underside of the body is naked (fig. 953), but in the adult there is a complete armour of bony scutes on this aspect.

Other genera of which some may perhaps be included in this family are *Amphibamus*, from the Carboniferous of Illinois; *Pelion*, from that of Ohio; *Batrachiderpeton*, from the Carboniferous of Britain; *Hylerpeton*, from that of Nova Scotia; *Dawsonia*, from the Permian of Bohemia; and *Sparodus*, from the latter deposits. *Batrachiderpeton* is remarkable for the absence of maxillary teeth, and the clustering of the palato-vomerine teeth; *Sparodus* presenting the latter feature, but retaining the maxillary teeth. The palatines of the latter genus are splint-like bones interposed between the vomers and maxillæ.

Family Apateonidæ.—In this family the skull (fig. 954) is triangular and comparatively narrow, while the teeth are marked by small grooves at their summits. The type genus *Apateon* is found in the Carboniferous rocks of Germany, while the allied *Melanerpeton* is from the Permian of Bohemia. An enlarged view of the dorsal aspect of the skull of the latter genus is shown in fig. 954, the retention of the internal gills indicating that it belonged to an immature individual.

Suborder 2. Aïstopoda.—In this remarkable group the body has a snake-like form, with well-developed ribs, but probably without either pectoral or pelvic girdles or limbs. The teeth are not folded; and Dr Fritsch considers that the external gills persisted throughout life.

Family Dolichosomatidæ.—This family, which is equivalent to both the *Plegothonidæ* and *Molgophidæ* of Professor Cope, is represented in the Carboniferous of Britain and the Permian of Bohemia by *Dolichosoma* and *Ophiderpeton*. In the former the skull is long and narrow, with no sculpture on the bones, and it is probable that the body was entirely naked; but in the latter the skull may have been shorter, and there was an armour on both surfaces of the body, the scutes on the ventral side being long oat-like splints, while those on the back were rounded and shagreen-like. The ossified gill-supports were furnished with small enamel-like denticules. One of the species of *Dolichosoma* attained a length of about two feet. *Plegethontia* and *Molgophis*, from the Carboniferous of Ohio, appear to be nearly related. *Palæosiren*, from the Permian of Bohemia, is a gigantic form provisionally included in this family,

of which the length is estimated at forty-five feet; while *Adenoderma* of the same deposits may indicate a distinct family.

From the many resemblances presented by the *Dolichosomatidæ* to the existing Apoda, Dr Fritsch considers it probable that they must be regarded as nearly related to the ancestral forms from which that group has been derived.

Suborder 3. Microsauria.—The Labyrinthodonts included in this suborder resemble Lizards in outward appearance, and have the centra of the vertebræ more or less elongated, and long, curved ribs.

Family Urocordylidæ.—This family—the *Nectridea* of Professor Miall and the *Ptyoniidæ* of Professor Cope—comprises stout, long-

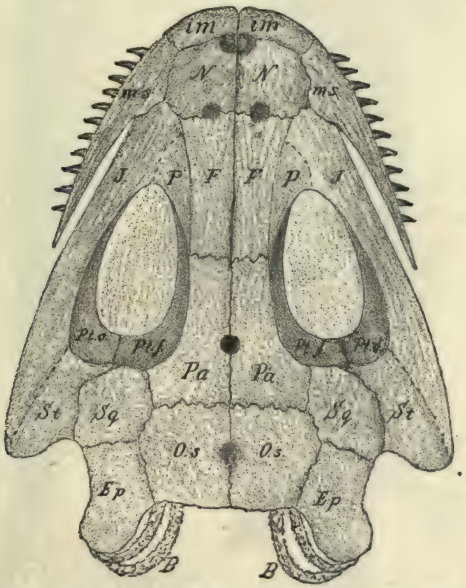


Fig. 954.—Upper surface of the skull of *Melanerpeton pusillum*; from the Permian of Bohemia; six times natural size. *B*, Branchiæ; *O.s.*, supra-occipital; other letters as in fig. 950. (After Fritsch.)

tailed forms, in which the epiotic cornua of the skull are much produced; the cranial bones are pitted; the neural spines and chevrons of the caudal vertebræ are much dilated at their extremities and pectinated; and caudal ribs are wanting. The type genus *Urocordylus*, as well as *Ceraterpeton*, occurs in the Carboniferous of Britain and Ohio, and also in the Permian of Bohemia; one species of the former attaining a length of about twenty inches. *Lepterpeton* is characteristic of the Carboniferous of Britain and Ohio; other

genera from the latter deposits being *Ptyonius*, *Œstocephalus*, *Hyphasma*, and probably *Sauropleura*.

Family Limnerpetidæ.—In the one genus *Limnerpeton*, of the Permian of Bohemia, the naked body is more elongated and the tail shorter than in the preceding family; the skull being broad and

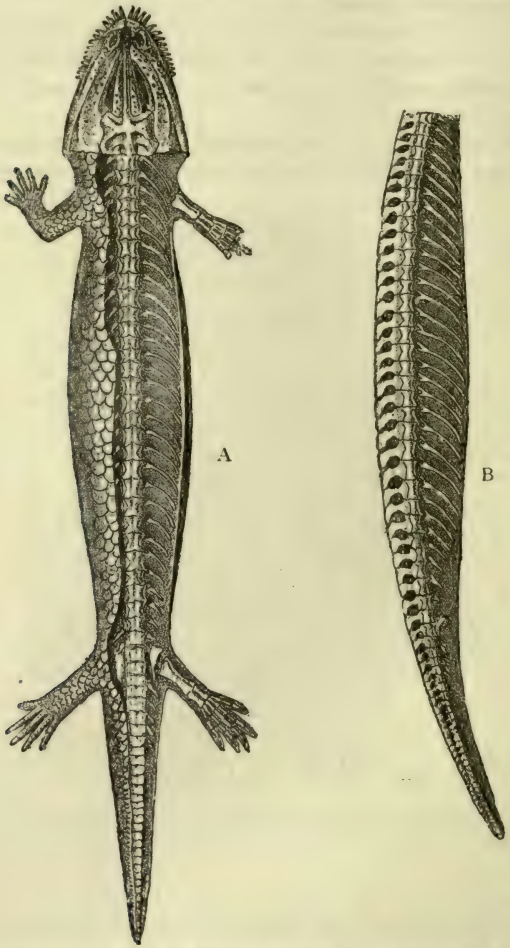


Fig. 955.– *Seeleya pusilla*; from the Permian of Bohemia. A, Under surface with scutes removed on the left side; and B, Right lateral view of the skeleton of the caudal region. Enlarged. (After Fritsch.)

Frog-like, with smooth bones; and the upper and lower processes of the caudal vertebræ simple. The teeth are small, with their summits either smooth or folded.

Family Hyloplesionidæ.—This family is readily recognised by the somewhat narrow head, the smooth cranial bones, and the envelopment of the whole body (fig. 955, A) in an armour of scutes. The caudal ribs (fig. 955) are well developed. It comprises the genera *Hyloplesion*, *Seeleya* (fig. 955), *Ricnodon*, and *Orthocosta*, from the Permian of Bohemia. *Hylonomus* and *Smilerpeton*, from the Carboniferous of Nova Scotia, are imperfectly known forms which may belong to the same family, in which case the name *Hylonomidæ* might be adopted. All the species are of small size.

Family Microbrachidæ.—This family includes small slender forms, with short pectoral limbs, strongly sculptured cranial bones, and scutes covering the entire body. The type genus *Microbrachis* occurs in the Permian of Bohemia, and has a long narrow skull. Three species are known. Another representative of this family is *Tuditanus*, of the Carboniferous of Ohio, characterised by its broad and expanded skull. *Cocytinus*, of the same deposits, may be provisionally placed in this family.

Suborder 4. Labyrinthodontia Vera.—The genera included in this group are characterised by their Crocodile-like bodies; the disk-like centra of the vertebræ, when these are fully ossified; by the vertebral column being, at least in the young, very generally of the types known as *rhachitomous* and *embolomerous;* by the teeth being more or less folded; and by the outer surface of the skull bearing a more or less strongly-marked sculpture, frequently accompanied by the presence of the so-called mucous canals. Some authorities divide this group into the *Temnospondyli* and *Stereospondyli*, according to the incomplete or complete ossification of the vertebral centra; but Dr Fritsch regards the whole series as constituting a single group—a view which is supported by the circumstance that in many of those forms in which the vertebræ are fully ossified in the adult, in the young stage their ossification is incomplete.

Before proceeding further it will be advisable to briefly consider the nature of the above-mentioned types of vertebral structure. In certain genera like *Diplospondylus*[1] (*Diplovertebron*) and *Cricotus* each caudal vertebra consists of an anterior centrum carrying the neural arch, and a posterior intercentrum to which the chevrons are united. These intercentra, according to the views of Professor Cope, correspond with the chevron-bearing intercentra of *Clepsydrops* among the Anomodont Reptilia, and the wedge-bones of *Sphenodon* among the Rhynchocephalians; this type of structure being known as the *embolomerous*. In the trunk vertebræ of other genera like *Trimerorhachis* (fig. 957) and *Archegosaurus* each vertebra (fig.

[1] This name has been proposed in lieu of the hybrid *Diplovertebron*.

956) consists of four portions—viz., a basal intercentrum (hypocentrum), a pair of pleurocentra, and a neural arch. In this *rhachitomous* type Professor Cope regards the pleurocentra as representing the centrum of the embolomerous type, since they both carry the arch; and as he finds that the functional centra in other forms, like *Chelydosaurus*, apparently correspond to the intercentra of *Archegosaurus*, while the pleurocentra are small and apparently about to disappear, it is argued that in other Amphibia the real centra are totally wanting, and the vertebral bodies, which in the caudal region have the chevrons united to them, are really intercentra, to which the neural arches have been shifted. Professor Cope regards the rhachitomous and embolomerous structures as characters of at least family value; but Dr Fritsch considers that the two types occur in different regions of one and the same species, as we

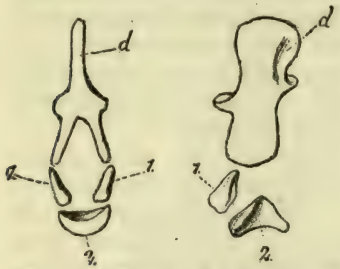


Fig. 956.—Diagram of a rhachitomous vertebra; from the front and left side. 1, Pleurocentra; 2, Intercentrum; *d*, Neural spine. (After Fritsch.)

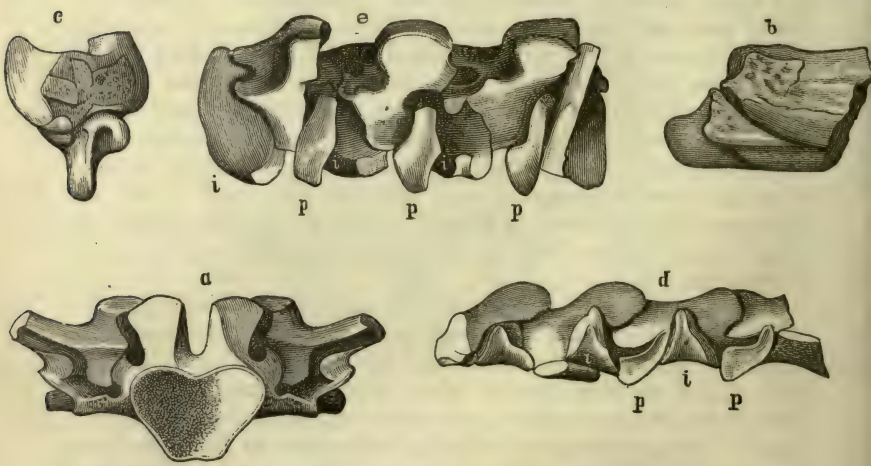


Fig. 957.—Parts of skull and vertebral column of *Trimerorhachis insignis*; from the Permian of North America. *a*, Basi- and exoccipitals; *b*, *c*, Lateral and posterior view of angle of mandible; *d*, *e*, Portions of vertebral column depressed by pressure; *i*, Intercentra; *p*, Pleurocentra. (After Cope.)

know to be the case in some of the Ganoid Fishes (*supra*, p. 959), where we find in *Eurycormus* and *Aspidorhynchus* a rhachitomous type of vertebræ in the cervical and dorsal regions, and an embol-

omerous type in the caudal. An excellent example of the rhachitomous type of vertebra is shown in fig. 960, the pleurocentra being omitted.

It should be observed that this interpretation of the homology of the rhachitomous vertebra is not accepted by Mr Hulke.

Family Archegosauridæ. — The well-known genus *Archegosaurus*, ranging in Europe from the Carboniferous to the Permian, may be taken as the type of a family, which for the present may include most of those forms in which the dorsal vertebræ are of the

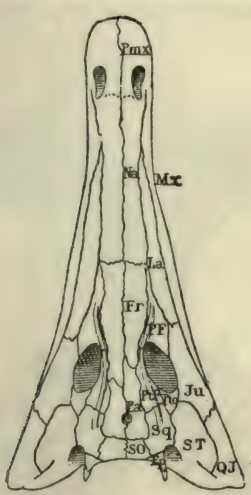


Fig. 958.—Upper surface of the cranium of *Archegosaurus;* from the Carboniferous. Reduced. *Pmx*, Premaxilla; *Mx*, Maxilla; *Na*, Nasal; *La*, Lachrymal; *Fr*, Frontal; *PF*, Prefrontal; *Pa*, Parietal; *PtF*, Postfrontal; *PtO*, Postorbital; *Ju*, Jugal; *QJ*, Quadratojugal; *Sq*, Squamosal; *ST*, Supratemporal; *Ep*, Epiotic; *SO*, Supraoccipital. (After Miall.)

Fig. 959.—Upper aspect of the right carpus of *Eryops;* from the Permian of North America. Reduced. *R*, Radius; *U*, Ulna; *r*, Radiale; *i*, Intermedium; *u*, Ulnare; c^1, c^2, c^3, Centralia; 1-5, Carpalia; i.-v., Metacarpals. (After Baur.)

rhachitomous type throughout life. Its members have, indeed, been split up into the *Melosauridæ*, *Trimerorhachidæ*, and *Eryopidæ;* but the observations of Dr Fritsch indicate that for the present at least such divisions are not definable. According to the last-named authority this family may be characterised as including Labyrinthodonts of medium dimensions; having cylindrical teeth of varying size, in which the folding of the dentine is comparatively slight; the upper surface of the skull being pitted; the supraoccipitals ridged; and the trunk vertebræ rhachitomous, and the caudal usually embolomerous. A ring of bones is usually developed in the sclerotic; the ventral surface of the body is always covered with

scutes; and the palatines form long splints lying on the inner side of the maxillæ. This family is evidently the most primitive one of the entire order; the vertebral column displaying an arrest of development at a stage which is transitional in higher forms. It is further remarkable for the small size of the coracoid, in which respect this group agrees with the Salamanders and some of the Anomodont Reptiles. The humerus has distinct condyles, as in the latter group; and in the pelvis the pubis is ossified, and, like that of some Anomodonts, unites with the ischium without the intervention of an obturator foramen. The tarsus and carpus (fig. 959) are

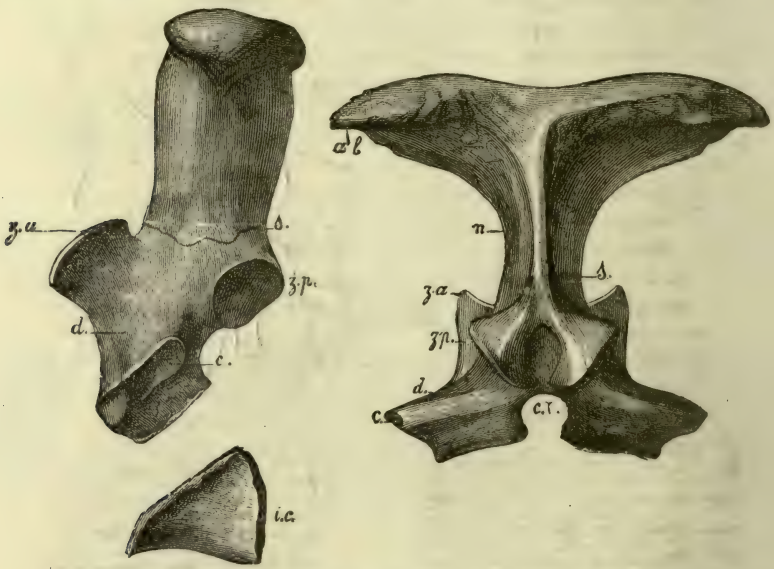


Fig. 960.—Left lateral aspect of the arch and intercentrum, and posterior aspect of the arch, of a dorsal vertebra of *Euchirosaurus Rochei*; from the Lower Permian of France. *n*, Neural spine, with lateral expansions, *al*; *s*, Suture between spine and arch; *z.a*, Pre-, *zp*, Postzygapophysis; *d*, Transverse process; *c*, Rib-facet; *c.r*, Neural canal; *i.c*, Intercentrum. (Adapted from Gaudry.)

characterised by the number of centralia, there being, according to the interpretation here followed, four of these bones in the former and three in the latter; and the first centrale articulating respectively with the tibia in the tarsus and with the radius in the carpus. This type of tarsal and carpal structure is evidently the most primitive yet observed.

In *Archegosaurus*, and also in *Zygosaurus* of the European Permian, and *Trimerorhachis* of the reputed equivalent strata of North America, the occipital condyles were not ossified; but they were

bony in many of the other genera. The following genera from the Permian of Europe have vertebræ agreeing in structure with those of the typical forms, and may be provisionally placed in the same family; they are named *Melosaurus*, *Osteophorus*, *Zygosaurus*, *Chelydosaurus*, *Cochleosaurus*, *Gaudrya*, *Actinodon*, and *Euchirosaurus*. *Sphenosaurus*, from the Permian of Bohemia, has also been placed here, although some writers regard it as a Reptile. The name *Discosaurus* has also been applied to a member of this group from the

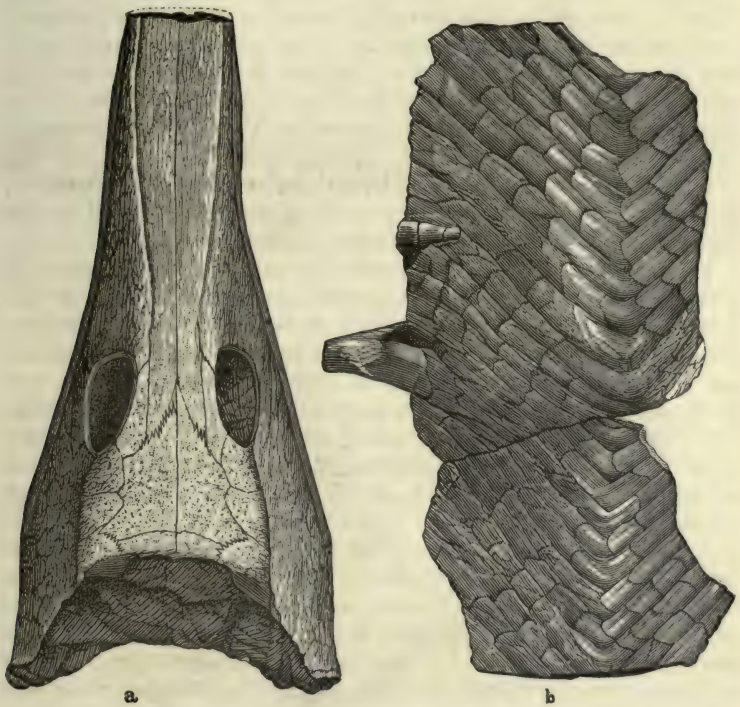


Fig. 961.—Upper surface of the skull (*a*), and ventral scutes (*b*) of *Cricotus heteroclitus*; from the Permian of North America. One-half natural size. (After Cope.)

Permian of Dresden, but it is preoccupied in the Sauropterygia. Portions of a vertebra of *Euchirosaurus*, from Autun in France, are shown in fig. 960, the neural spine being remarkable for the great lateral expansion of its summit; according to Dr Fritsch's restoration (fig. 956) the pleurocentra belonging to this vertebra would be on the anterior side, but Dr Zittel would rather regard those on the posterior aspect as referable to this segment of the column. In the Bijori stage of the Lower Gondwanas of India this group is

represented by *Gondwanosaurus;* while, if we may judge by a detached intercentrum which may belong to it, *Rhytidosteus*, of the Karoo system of South Africa, should also find a place here. The American Permian, in addition to *Trimerorhachis*, has also yielded *Zatrachys*, *Eryops*, *Acheloma*, and *Anisodexis*. *Eryops* includes very large species, in which the nares are widely separated and not placed at the extremity of the snout, and the thoracic plates are not sculptured.

Family Diplospondylidæ.—This family[1] is proposed by Dr Fritsch for the genus *Diplospondylus*, from the Permian of Bohemia, characterised by the embolomerous structure of the entire vertebral column, and the absence of pits on the skull. *Cricotus* (fig. 961), from the Permian of Illinois and Texas, appears to be an allied form, which Professor Cope makes the type of the family *Cricotidæ*.

Finally, it may be mentioned here that the genus *Ichthyacanthus*, from the Carboniferous of Ohio, which is frequently placed in the Microsauria, is described as having rhachitomous vertebræ.

Family Nyraniidæ.—The genus *Nyrania*, from the Permian of Bohemia, of which the skull is shown on an enlarged scale in figs. 824, 825 (pp. 902, 903), differs from *Archegosaurus* in that the palatines, in place of forming splints on the inner side of the maxillæ, are situated near the middle line, internally to the vomers and pterygoids, and would therefore seem to represent a distinct family. This arrangement of the bones of the palate is similar to that obtaining in the existing Caudata. Some of the genera noticed among the *Archegosauridæ*, in which the skull is unknown, may belong to this family.

Family Dendrerpetidæ.—This family, which may be taken to include the Brachiopina of Professor Miall, contains several genera, of which the precise serial position and full affinities are at present somewhat uncertain. The skull is parabolic, and marked by deep pits; the parasphenoid in the type genus has a short stem; and the teeth have irregular foldings at the base. The vertebræ were fully ossified, and may have been of the embolomerous type. The type genus *Dendrerpeton* is a medium-sized form occurring in the Carboniferous of Nova Scotia and the Permian of Bohemia, and characterised by the orbits being placed near the centre of the skull. Another group of genera, constituting the above-mentioned Brachiopina, appears to agree so closely with the type in cranial characters, that it may at least provisionally be included in the same family. The orbits are generally placed somewhat anteriorly. This group comprises *Brachyops*, known by a single skull from the Mangli stage of the Upper Gondwana system of India; *Micropholis* (*Petrophryne*),

[1] *Diplovertebridæ*, see note, p. 1027.

from the Karoo system of South Africa; *Bothriceps*, from the Lower Mesozoic of Australia; and *Rhinosaurus*, from the Jurassic of the Ural Mountains. There is frequently a *lyra* on the skull, but this

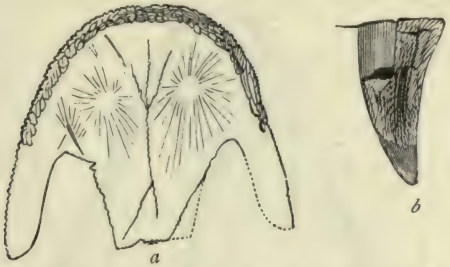


Fig. 962.—*a*, Oral view of palate, much reduced, *b*, Tooth, natural size, of *Baphetes planiceps*; from the Carboniferous of Nova Scotia.

is wanting in *Micropholis*, as in *Dendrerpeton*. It is probable that a young skeleton from the Lower Mesozoic Hawkesbury beds of New South Wales, described under the preoccupied name of *Platyceps*, belongs to *Bothriceps*.

Family Anthracosauridæ.—In this family the vertebral column is fully ossified in the adult; the teeth are deeply infolded; the mucous canals between the orbits and the nares form a lyre-shaped pattern known as the *lyra*; and the ventral surface of the body typically has a covering of bony scutes. The skull may be parabolic, but is usually triangular. This family may be divided into three subfamilies. The first, or *Baphetinæ*, is represented solely by the genus *Baphetes*, of the Carboniferous of Nova Scotia, which can only be provisionally placed in this family. It is only known by the imperfect skull (fig. 962), which is broad, and rounded anteriorly.

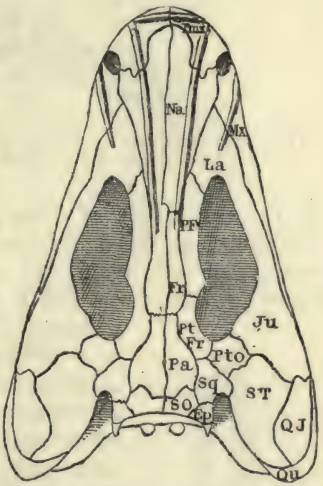


Fig. 963.—Upper view of the skull of *Loxomma Allmanni*; from the Carboniferous of Durham. Reduced. Letters as in fig. 958. (After Miall.)

In the *Loxommatinæ* (*Chauliodontia*), the members of the one genus *Loxomma* attain a large size, and are characterised by the triangular skull (fig. 963), which has large posterior projections, with the lyra forming two straight grooves, continued posteriorly as ridges. The teeth are compressed, large, and irregular, with the foldings deeper

than in the *Archegosauridæ*. The vertebral centra are disk-like, and may perhaps be embolomerous. *Loxomma* (fig. 963) occurs in England in the Carboniferous, but has also been recorded

Fig. 964.—Dorsal surface of the skull of *Anthracosaurus Russelli*; from the Carboniferous of England. One-sixth natural size. (After Atthey.)

from the Permian of Bohemia. The large size of the orbits is well shown in the figure; another characteristic feature being the absence of a postglenoidal process to the mandible. The ventral scutes are unknown, and if it be eventually found that these are wanting, this genus should perhaps form the type of a distinct family. In the typical subfamily *Anthracosaurinæ* the skull (fig. 964) is triangular, and characterised by the small size of the palatal vacuities; while the teeth are subcylindrical. The type genus *Anthracosaurus* occurs, as its name implies, in the Carboniferous, ranging from Britain to the Continent. One of the dermal ventral scutes is shown in fig. 965. The skull was also covered with scales or scutes; and it appears from one specimen that these scutes did not extend over the parietal foramen, which induces Dr Credner to consider that the Palæozoic Labyrinthodonts were provided with a functional parietal eye, of which an aborted rudiment persists in *Sphenodon*. The imperfectly

Fig. 965.—Scute of *Anthracosaurus*. (After Atthey.)

known *Dasyceps*, from the English Permian, is allied in cranial structure to *Anthracosaurus*. Moreover, some writers place in this family the imperfectly known genera *Platyops*, from the Permian of Russia, and *Macromerion*, from the corresponding strata of Bohemia.

Family Mastodonsauridæ.—The members of this family, together with some of the *Anthracosauridæ*, constitute the Euglypta of Professor Miall's classification, and may be regarded as the typical representatives of the order. They are distinguished from the latter family by the still more complex structure of the teeth; the stronger sculpture of the skull; and the absence of scutes on the ventral surface of the body. Large palatovomerine teeth (fig. 966) are placed on the inner side of the maxillary teeth, and there is a corresponding inner series of small teeth in

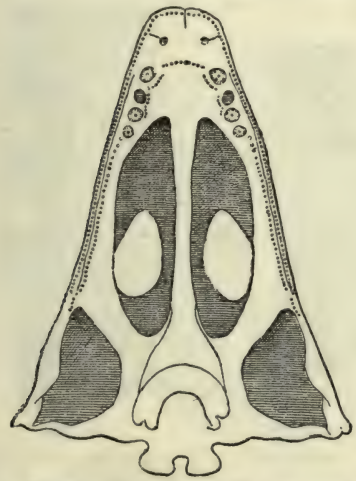


Fig. 966.—Palatal aspect of the cranium of *Mastodonsaurus giganteus*; from the Keuper of Würtemberg. Reduced. (After Miall.)

Fig. 967.—*Mastodonsaurus giganteus*. *a*, Dorsal aspect of skull, greatly reduced; *b*, tooth on a larger scale.

the mandible; while there is no bony ring in the sclerotic. The following features may be also noticed, although some of them are common to the typical *Anthracosauridæ*. The mandible has a large postglenoidal process, and the crowns of the teeth are conical. The palatines have the same position as in the *Archegosauridæ*. In the pelvis of the type genus the pubes are separate from the ischia, and do not enter into the formation of the acetabulum; and the sacral ribs form kidney-like disks. The centra or bodies of the vertebræ in the adult form disks which are fully ossified; but in the

young, as we infer from *Mastodonsaurus*, in which alone this feature has been observed, they were rhachitomous, as in the adult condition of the *Archegosauridæ*. The palatal vacuities were large and approximated, as is well shown in fig. 966. This family may be divided into two groups, according to the presence or absence of an inner articular buttress at the proximal extremity of the mandible. The group in which this buttress is present is represented by the type genus *Mastodonsaurus*, best known by the huge *Mastodonsaurus giganteus* (figs. 966, 967) of the Trias of Europe, which probably attained a length of seven or eight feet, and ranged from the Muschelkalk to the Rhætic. Besides other European Triassic species, this genus is also represented in the Lower Mesozoic (Maleri stage) of India by a form closely allied to *M. giganteus*, and by another in the Hawkesbury beds of New South Wales. Figure 968 shows the

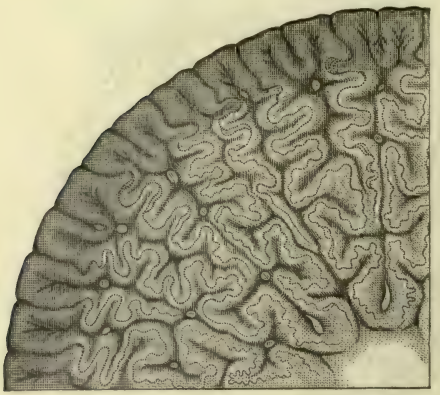


Fig. 968.—Transverse section of a segment of a tooth of *Mastodonsaurus giganteus*. Greatly enlarged. (After Owen.)

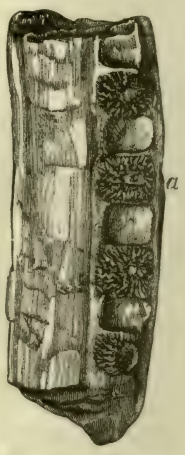


Fig. 969.—Fragment of jaw of one of the *Mastodonsauridæ*; from the Upper Gondwanas of India. *a* shows the section of a tooth.

structure of a transverse section of a segment of a tooth of this genus; the mode of attachment of the teeth to the jaw being exhibited in fig. 969. In the transverse section it will be observed that there is one set of sinuous linear interspaces communicating with the exterior, and a corresponding series (separated from each other by the dental wall) of sinuous processes from the central pulp-cavity. Other genera of this group are *Capitosaurus* (including *Cyclotosaurus*), from the Keuper of Germany; *Trematosaurus*, from the Bunter of the same country, distinguished by its more slender

skull; and the apparently allied *Gonioglyptus*, from the Panchet stage of the Lower Gondwanas of India. *Pachygonia* (fig. 952), of the latter deposits, may also be provisionally included in this group. From the Maleri stage of the Upper Gondwanas we have also a Labyrinthodont apparently closely allied to *Capitosaurus*, and thus indicating a precise parallelism in the evolution of the group in the Indian and European horizons. Here also we may perhaps place a small form described under the provisional name of *Glyptognathus*, from the Indian Panchets. *Metopias*, of the Continental Keuper and Rhætic, is distinguished from the preceding genera by the more anterior position of the orbits; *Labyrinthodon*, of the English Keuper, being probably allied. The second group is represented by *Diadetognathus*, of the Warwickshire Trias, in which the mandible has no inner articular buttress.

Of Uncertain Family.—Here may be mentioned the genus *Eosaurus*, founded upon large vertebral centra (fig. 970), from the

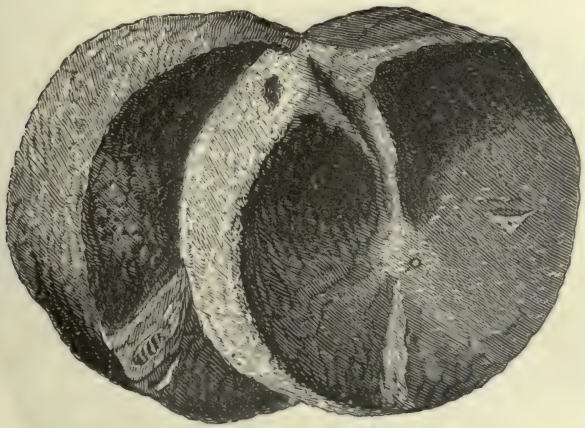


Fig. 970.—Two vertebral centra of *Eosaurus acadianus*; from the Carboniferous of Nova Scotia. (After Marsh.)

Carboniferous of Nova Scotia, which were regarded by Professor Marsh as belonging to an Ichthyosauroid Reptile, but which really indicate a large Labyrinthodont, perhaps referable to the *Mastodonsauridæ*.

Leaving out some ill-defined genera, mention must be made of *Pteroplax*, of the British Carboniferous, which was formerly classed next to *Batrachiderpeton*. The skull is elongated, and remarkable for the incomplete orbits; while it appears that many of the ordinary bones are wanting. The cranial bones have a pitted sculpture; and the vertebral centra are thick and fully ossified.

Labyrinthodont Footprints.—In the Bunter, or Lower Trias of Germany, and also in the Keuper, or upper division of the same system in Cheshire and Warwickshire, there are frequently found long series of the impressions of the feet of five-toed animals, which have generally been regarded as those of Labyrinthodonts, although it has been suggested by Professor Miall that some of them may be Dinosaurian. These footprints were described under the name of *Chirotherium*, on the supposition that they were of Mammalian origin; but in case this should prove incorrect the alternative name *Chirosaurus* was proposed, and since they are certainly Saurian, the

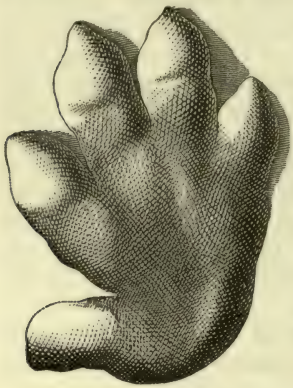


Fig. 970*bis*.—Footprints of *Chirosaurus Barthi*, from the Bunter sandstone of Hessberg, near Hildburghausen, Germany. Reduced.

latter name should be adopted. These impressions (fig. 970 *bis*) were made by Saurians in which the hind foot was much larger

than the fore foot, some of those of the hind foot having a length of eight inches. The absence of any known Dinosaurians from the Bunter is strongly in favour of the Labyrinthodont nature of these tracks; and it has been suggested that those described as *Chirosaurus Barthi* were made by *Trematosaurus Brauni* of the Bunter, the skull of which has a length of eight inches. If this should prove to be the case, the name *Trematosaurus* would have to yield to the earlier *Chirosaurus*. The largest tracks from the Keuper of Cheshire have been described as *C. Herculis*. Other tracks of feet from the Permian and Trias, which may be of Labyrinthodont origin, have been described under distinct names which it will be unnecessary to quote.

Order II. Apoda.—The remarkable limbless Cæcilians being unknown in a fossil state require no further mention.

Order III. Caudata.—In this order the body is elongate, and either lacertiform or anguiform, with a tail, and usually with two, but occasionally only one, pairs of limbs. The cranium lacks the postorbital, supratemporal, and supraoccipital bones of the Labyrin-

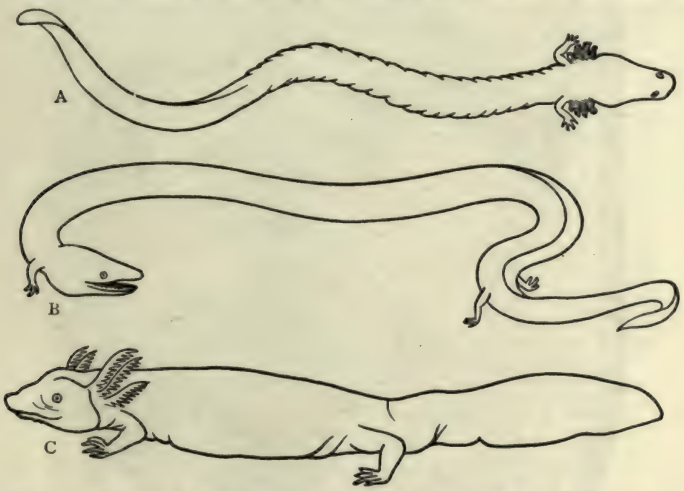


Fig. 971.—Outlines of *Siren* (A), *Amphiuma* (B), and *Menobranchus* (C). Reduced. (After Mivart.)

thodontia, and the palatines are approximated to the middle line, and placed internally to the vomers and pterygoids. The ribs are short, and the bodies of the vertebræ are either amphi- or opisthocœlous. The resemblance in the contour of the skull and the short ribs to the *Protritonidæ* suggests an affinity between the two groups; but the position of the palatines is rather indicative of a relationship with the *Nyraniidæ*.

Family Hylæobatrachidæ.—This family is formed for the

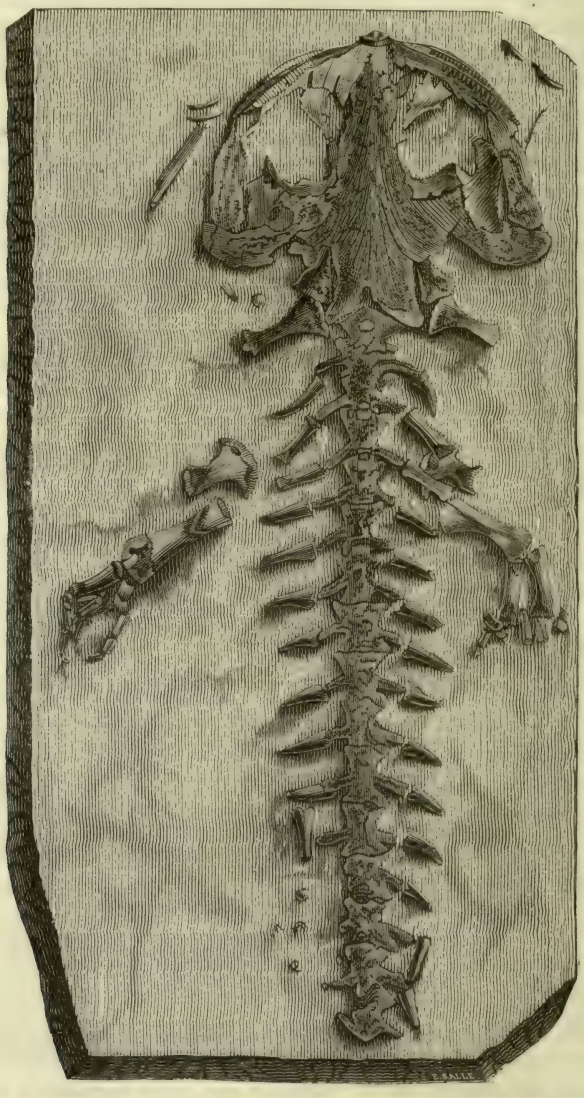


Fig. 972.—Anterior part of the skeleton of *Megalobatrachus Scheuchzeri*; from the Upper Miocene of Switzerland. Reduced.

reception of *Hylæobatrachus*, from the Wealden of Belgium, which appears to be an ancestral form allied to the *Proteidæ*, but distin-

guished by the presence of a maxilla, and of five digits to the feet.

Families Sirenidæ and Proteidæ.—*Siren* (fig. 971, A) and *Proteus*, together with *Menobranchus* (*ibid.*, C) are characterised by the persistent gills, the absence of maxillæ, the amphicœlous vertebræ, and the reduction of the number of the digits below five; *Siren* differing from the other two by the absence of pelvic limbs. No fossil representatives are known.

Family Amphiumidæ.—In this family the gills are shed, and maxillæ are present; but it agrees with the two last in the amphicœlous vertebræ, the cartilaginous carpus and tarsus, and the absence of eyelids. In the typical North American genus *Amphiuma* (fig. 971, B) the body is much elongated, and the limbs are very short. Another American genus is *Menopoma*, allied to which is *Megalobatrachus* (*Cryptobranchus* or *Sieboldia*), typically represented by the Gigantic Salamander (*M. maximus*) of China and Japan, and in which we may probably include the large Salamander (fig. 972) from the Upper Miocene of Switzerland, originally regarded as human, and subsequently described under the name of *Andrias*.

Family Salamandridæ.—The true Salamanders lose their gills, although there are instances, as in *Amblystoma* (*Siredon*), where they persist in some individuals. Eyelids are present; the vertebræ are generally opisthocœlous; and the carpus and tarsus more or less ossified. This family is now represented in Europe by the Salamanders (*Salamandra*) and Newts (*Molge* or *Triton*). In a fossil state the existing *Molge cristata* (fig. 973) occurs in the Norfolk

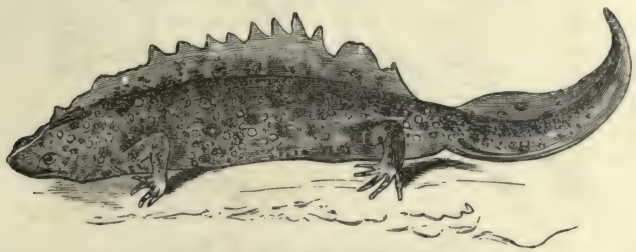


Fig. 973.—The Crested Newt (*Molge cristata*).

Forest-bed, and representatives of this genus have also been recorded from the Middle and Lower Miocene of the Continent. The latter deposits have also yielded remains referred to *Salamandra*, while the name *Chelotriton* has been applied to an imperfectly known form from the Lower Miocene of St Gérand-le-Puy, in Allier. *Heliarchon*, from the corresponding strata of Rott, near Bonn, is allied to *Salamandra*, and may not improbably be identical with *Chelotriton*. *Megalo-*

triton is a large form from the Upper Eocene Phosphorites of Central France.

Order IV. Ecaudata.—The Frogs and Toads form a highly specialised order of comparatively late origin. In the adult the body is short, destitute of a tail, and furnished with four limbs, of

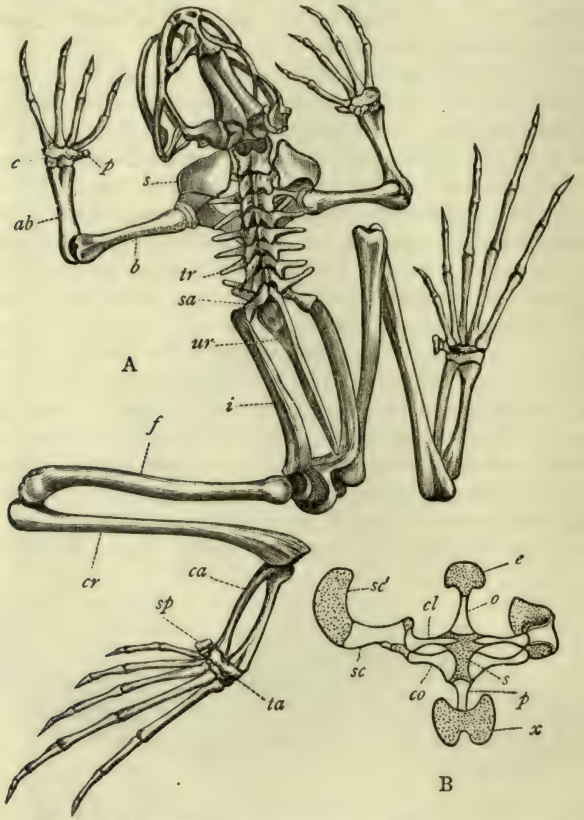


Fig. 974.—A, Skeleton of the Frog (*Rana temporaria*): *tr*, Transverse processes of vertebræ; *sa*, Sacrum; *ur*, Urostyle; *i*, Ilium; *s*, Suprascapula; *b*, Humerus; *ab*, Radius and ulna; *c*, Carpus; *p*, Pollex; *f*, Femur; *cr*, Tibia and fibula; *ca*, Calcaneo-astragalus; *ta*, Tarsus; *sp*, Prohallux. B, Pectoral arch and sternum of Frog (after Gegenbaur). The dotted parts represent cartilages. *e*, Episternum; *o*, Omosternum; *p*, Body of the sternum; *x*, Xiphisternum; *sc'*, Suprascapula; *sc*, Scapula; *cl*, Precoracoid; *co*, Coracoid; *s*, Epicoracoid.

which the pelvic pair is the longer, and adapted for leaping. There are no gills. The skull is short and wide, with enormous orbits, and the parietals confluent with the frontals. A peculiar ossification known as the *girdle-bone* encircles the skull in the ethmoidal region, and there is a predentary ossification in the mandible. The pre-

sacral vertebræ are few in number, and generally procœlous; there is but one vertebra in the sacrum; the vertebral column terminates in a long urostyle (fig. 974, *ur*), and there are usually no separate ribs. The ilia (*i*) are prolonged backwards, so as to throw the acetabulum far behind the sacrum; the radius and ulna (*ab*), and the tibia and fibula (*cr*) are respectively fused together; and the calcaneum and astragalus (*ca*) greatly elongated. There are five digits in each foot, with an additional ossicle (*sp*) in the pes which apparently represents a prohallux.

According to the presence or absence of the tongue this order is divided into the suborders Phaneroglossa and Aglossa; the latter containing only the two families *Dactylethridæ* and *Pipidæ*. The Phaneroglossa are subdivided into the *Firmisternine* and *Arciferine* series; the former characterised by the epicoracoids forming a band connecting the coracoids (fig. 974, B), and the latter by the overlapping of the epicoracoids. Since fossil forms are but very imperfectly known, only brief mention will be made of those families which have fossil representatives.

Family Discoglossidæ.—Commencing with the *Arciferine* series of the Phaneroglossa the present family is distinguished from those that follow, and thereby approximates to the Newts, in having opisthocœlous vertebræ and rudimentary ribs. The European genus *Bombinator* is probably represented in the Upper Miocene of Switzerland; although some writers have referred the fossil species to a distinct genus under the name of *Pelophilus*. Opisthocœlous vertebræ from the Middle Miocene of Sausan, in Gers, may belong either to *Bombinator* or to the other existing European genus *Alytes*. *Bufavus*, from the Middle Tertiary of Italy, is said to present many affinities to the present family, but in the absence of ribs approximates to the one that follows.

Family Pelobatidæ.—This small family is characterised by the presence of teeth in the upper jaw; the absence of ribs; and the unexpanded extremity of the sacral rib. The vertebræ are usually procœlous, although occasionally opisthocœlous. The existing genus *Pelobates* occurs in the Miocene of Sausan, while the imperfectly known *Protopelobates*, from the Miocene of Bohemia, may belong either to this or the next family.

Family Palæobatrachidæ.—This extinct family has teeth in the upper jaw; no ribs; expanded ribs to the sacral vertebra; and procœlous vertebræ. The single genus *Palæobatrachus* (*Probatrachus*) is now known to have been widely distributed over the Continent during the Lower Miocene; more than a dozen species having been described.

Family Bufonidæ.—The true Toads are characterised by the total absence of teeth and dorsal ribs; the expanded extremities of

the ribs of the sacral vertebra; and the procœlous vertebræ. Of the type genus *Bufo* existing species occur in the European and Indian Pleistocene. *B. Gessneri*, of the Upper Miocene of Switzerland, appears closely allied to the living *B. viridis*, although, together with another species from the same beds, it has been made the type of *Palæophrynus*. Dr Filhol records the type genus from the Upper Eocene Phosphorites of France.

Family Cystignathidæ.—This family represents the Frogs in Tropical America and Australia. The huge *Ceratophrys cornuta*, or Horned Frog of Brazil, occurs in the cave-deposits of that country; while *Latonia*, of the Swiss Miocene, appears to be a closely allied if not identical genus, characterised by the smaller head, more slender pelvis, shorter manus, and longer pes. A somewhat similar instance of distribution occurs in the case of the Chelonian *Chelydra*. The cave-deposits of Brazil have also yielded remains of the existing *Leptodactylus pentadactylus*.

Family Ranidæ.—In the *Firmisternine* series the True Frogs have teeth in the upper jaw, and the extremities of the sacral ribs are not expanded. *Rana* is represented by existing species in the Norfolk Forest-bed, and probably in the Pleistocene of Sardinia; it probably also occurs in the Miocene of Sausan and other places on the Continent; and has been described from the Upper Eocene Phosphorites of Central France, where the one known species seems to be allied to the Indian *R. tigrina*. The Oriental genus *Oxyglossus*, in which there are no vomerine teeth, is found in the Eocene of Bombay. *Ranavus*, from the Middle Tertiary of Italy, may perhaps belong to this family, although it is said to show affinity to the *Pelobatidæ;* and we may here mention the imperfectly known *Amphirana*, *Batrachus*, and *Protophrynus* of the Lower Miocene of France, although their family position may be doubtful.

LITERATURE OF AMPHIBIA.

1. Atthey (T.)—"On *Anthracosaurus Russelli*." 'Ann. Mag. Nat. Hist.,' ser. 4, vol. xviii. (1876).
2. Baur (G.)—"Die alteste Tarsus (*Archegosaurus*)." 'Zool. Anzeiger.' No. 216. (1886).
3. Burmeister (H.)—"Die Labyrinthodonten aus dem Bunten Sandstein im Bernburg." 1849.
4. Cope (E. D.)—"Description of Extinct Batrachia and Reptilia from the Permian of Texas." 'Proc. Amer. Phil. Soc.,' vol. xvii. (1878).
5. —— "On the Intercentrum of the Terrestrial Vertebrata." 'Trans. Amer. Phil. Soc.,' vol. xvi. (1886).
6. —— "Synopsis of Extinct Batrachia from the Coal-Measures." 'Geol. Surv. of Ohio, vol. ii., Palæontology' (1875).

7. COPE (E. D.)—"The Batrachia of the Permian of North America." 'American Naturalist,' vol. xviii. (1884).
8. CREDNER (H.)—"Die Stegocephalen aus dem Rothliegenden des Plauen'schen Grundes bei Dresden." 'Zeitschr. deutsch. geol. Ges.,' vols. xxxiii.-xxxviii. (1881-86).
9. DAWSON (W.)—"Acadian Geology." 2d ed. 1867.
10. —— "Air-breathers of the Coal-Period." 1863.
11. DOLLO (L.)—"Note sur le Batrachien de Bernissart." 'Bull. Mus. R. Hist. Nat. Belg.,' vol. iii. (1884).
12. EMBLETON (E.) and ATTHEY (A.)—"On the Skull and some other Bones of *Loxomma Allmanni*." 'Ann. Mag. Nat. Hist.,' ser. 4, vol. xiv. (1874).
13. FRAAS (E.)—"Die Labyrinthodonten der schwäbischen Trias,"—'Palæontographica,' vol. xxxvi. (1889).
14. FRITSCH (A.)—"Fauna der Gaskohle und der Kalksteine der Permformation Böhmens." Prague (1883-86).
15. GAUDRY (A.)—"Les Enchaînements du Monde Animal, &c.—Fossiles Primaires." Paris (1883).
16. —— "Les Reptiles de l'Epoque Permienne aux Environs d'Autun." 'Bull. Soc. Géol. France,' ser. 3, vol. vii. (1878).
17. —— "L'Actinodon." 'Archiv. Mus. Hist. Nat., Paris,' vol. x. (1887).
18. HUXLEY (T. H.)—"New Labyrinthodonts from the Edinburgh Coalfield." 'Quart. Journ. Geol. Soc.,' vol. xviii. 1862.
19. —— "Description of Vertebrate Remains from the Jarrow Colliery, Kilkenny." 'Trans. Roy. Irish Academy,' vol. xxiv. (1867).
20. —— "Vertebrate Fossils from the Panchet Rocks." 'Palæontologia Indica (Mem. Geol. Surv. Ind.),' ser. 4, vol. i. (1865).
21. LYDEKKER (R.)—"The Bijori Labyrinthodont." 'Palæontologia Indica,' ser. 4, vol. i. (1885).
22. MIALL (L. C.)—"Report on the Labyrinthodonts of the Coal-Measures." 'Rep. Brit. Assoc.' 1873.
23. —— "Report on the Structure and Classification of the Labyrinthodonts." *Ibid.* 1874.
24. OWEN (R.)—"Fossil Reptilia discovered in the Coal-Measures of South Joggins, Nova Scotia." 'Quart. Journ. Geol. Soc.,' vol. xviii. (1862).
25. —— "On a Labyrinthodont Amphibian (*Rhytidosteus*) from the Cape of Good Hope." *Ibid.*, vol. xl. (1884).
26. PORTIS (A.)—"Resti di Batraci Fossili Italiani." 'Appunti Paleontologi,' part 2. Turin (1885).
27. ZITTEL (K. A.)—"Handbuch der Palæontologie," Abth. i., vol. iii., part 2. Munich (1888).

CHAPTER LII.

CLASS REPTILIA.

General Structure.

With the Reptiles we enter upon the consideration of the first of two classes which, from the possession of many common characters, have been brigaded together by Professor Huxley under the name of Sauropsida. The name Monocondylia had, however, been previously proposed by Hæckel for these two classes, and some writers consequently prefer to use this term. These two classes are the Reptilia and the Aves, or Birds; and although recent research has shown the existence of a close affinity between the more generalised Reptilia and the Amphibia, and thus with the Mammalia, yet it has in no wise tended to interfere with this association. It should, however, be observed that since it is probable the Reptiles have taken origin from forms more or less nearly allied to some of the earlier Amphibia, with which we are at present acquainted, it is obvious that there must once have existed animals in which the characteristic features of the true Amphibia and the Reptilia were more or less blended, and that the practicability of drawing a distinction between the two classes is thus (as in other cases) more or less due to the imperfection of our knowledge. With this proviso, and bearing in mind that some of the more generalised forms with which we are even now acquainted may not conform in every detail with the undermentioned characters, the Reptilia as a whole, together with the Birds, may be distinguished from the preceding classes on the one hand, and from the Mammalia on the other, by the following features.

Epidermal structures in the form of scales or feathers are generally present, but there are never hairs. The vertebræ, which are ossified, usually have no epiphyses.[1] The basioccipital, with one

[1] These are present in some of the Sauropterygia among Reptiles, and in Parrots among Birds.

or two exceptions, is completely ossified; and, in conjunction with the exoccipitals, forms the single occipital condyle by which the cranium articulates with the atlas vertebra. In the adult there is, as a rule, no distinct parasphenoid [1] on the base of the skull. The mandibular rami respectively consist of an articular cartilage-bone and of several membrane-bones; the articular bone being connected with the squamosal of the cranium by a quadrate. The apparent ankle-joint, in all existing forms, is situated between the proximal and distal rows of the tarsus; and not, as in the Mammalia, between the tibia and astragalus. Gills are never developed during any period of life; the embryo is provided with an amnion and an allantois; and there are no mammary glands. As the palæontologist will not have to deal with the other distinctive features derived from the soft parts, it will not be necessary to refer to them in this work.

Regarding the features of Reptiles as distinct from Birds, the approximation between the two classes is so close that it is difficult to give any very clear diagnosis. In the present class, however, the epidermal structures take the form of overlapping horny scales (Squamata), or of shields with their edges in apposition (Chelonia); while dermal bony scutes are very frequently developed. The vertebræ may be amphicœlous, opisthocœlous, or procœlous; but the centra of the cervicals do not have cylindroidal and saddle-shaped articular surfaces. The sacral vertebræ, when present, have broad expanded ribs for articulation with the ilia. The sternum in existing forms is rhomboidal; and the ribs may be attached to it by a backward median process, or processes. The interclavicle is never fused with the clavicles. There are more than three digits in the manus; and never less than three in the pes. Except in the Theromorous branch, the three elements of the pelvis as a rule remain distinct; [2] and there is apparently no known instance, except one which may probably be regarded as a pathological peculiarity, of the fusion of the metatarsals, or of their union with the distal row of the tarsus. In all living Reptiles there is both a right and a left aortic arch; the arterial and venous circulations are at best but imperfectly separated; and the blood is cold.

Since the various orders of Reptiles differ so greatly from one another in structure it will be advisable to make most of our observations on their osteology under those several headings. As a rule, however, the bones of the cranium retain the general arrangement observable in the Amphibia; there being distinct postorbital or postfrontal ossifications; usually either one or two temporal arcades; and distinct post-, supra-, and infratemporal fossæ, as defined in the

[1] Dr Baur suggests that this bone may be present in *Palæohatteria*.

[2] They are anchylosed in *Testudo atlas* of the Indian Siwaliks, and also in *Miolania*.

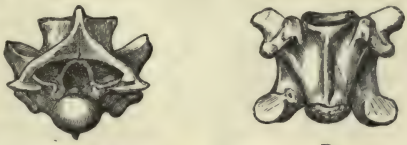
introductory chapter (p. 904). The bones of the skull are of a dense ivory-like structure, and in most cases their sutures persist; although in certain groups the premaxillæ, frontals, and parietals may respectively unite. A new element—the *transverse*, or *transpalatine*, bone (fig. 1089, *Ts*)—connecting the maxilla with the pterygoid, appears; but this is absent in the Chelonia and some Ophidia. An *epipterygoid*, or *columella*, connecting the pterygoid with the parietals, may also be present. A parietal foramen may or may not be present; and the occipital condyle is usually placed at the hinder extremity of the cranium. The apertures of the external nares may be terminal, as in the Amphibia, or approximated to the orbits, as in the Birds; and the bones of the palate may develop a floor underlying the narial passage and thus cutting it off from the mouth. As a general rule the mandibular symphysis is not anchylosed; but this takes place in the Chelonia and Ornithosauria. The quadrate may be either loosely or immovably attached to the cranium.

The dentition is usually well developed, and the teeth of different parts of the jaws are occasionally more or less differentiated; although there is no known instance where they are implanted by double roots, or where their crowns have deep infoldings of enamel. They may be present not only in the jaws, but also upon the palatine, pterygoid, and more rarely the vomer. In other instances, however, teeth may be entirely wanting, and the jaws simply ensheathed in horn. The teeth may be anchylosed to the outer side of the jaws, when the dentition is termed *pleurodont* (fig. 975); or to their summits, when the term *acrodont* is applied; or they may be set in a groove, with or without anchylosis to the bone; or, finally, they may be placed in distinct sockets, when the dentition is said to be *thecodont*. The teeth on the palate are generally anchylosed to the subjacent bones. There is usually a continuous succession of teeth developed throughout life; the new teeth coming up beneath those in use and absorbing the base of the crown, as is shown in the teeth of the Gharial represented in fig. 1090. In shape the teeth of Reptiles present great variation; but a very common type, from which many of the variations are derived, consists of a more or less laterally-compressed and recurved cone, with fore-and-aft cutting edges, or *carinæ*, which may or may not be serrated (fig. 976). Occasionally, however, the teeth of the jaws or those of the palate may have nearly flat crowns adapted for crushing (fig. 986).

Fig. 975.—Inner view of the left ramus of the mandible of *Iguana*.

When both pairs of limbs are present the vertebral column is differentiated into cervical, dorsal, lumbar, sacral, and caudal regions; and the vertebræ themselves are invariably ossified, although in some primitive types a small notochordal canal may perforate their centra. In a large number of existing forms the majority of the centra are procœlous; but they are amphicœlous in many fossil and a few existing types; while among the Dinosauria and Chelonia an opisthocœlous type is common in parts of the series. In all cases there is an intercentrum between the skull and the atlas; which may either form the inferior ring of the latter, or, when the centrum of the atlas is separate (Ichthyopterygia), may be of the normal wedge-like form. In some groups additional articulations may be developed on the arches of the trunk vertebræ, taking the form of a wedge-shaped process, or *zygosphene*, fitting into a corresponding cavity, or *zygantrum* (fig. 977). The transverse processes of the dorsal vertebræ may be either long (fig. 1058) or very short (fig. 977); and the ribs may articulate either by a single head with the transverse process, or by two heads to different portions of the same process, or by one articulation to the latter and by another to a facet on the arch or the centrum; there being great variation as to the position of the transverse processes and rib-facets in different groups, and also in the different parts of the column of a single animal. Occasionally the ribs articulate at the junction of two vertebræ. Chevron-bones are generally present in the tail; and intercentra may be retained. No living Reptile with limbs has less than two sacral vertebræ, and in certain extinct forms the number may be increased to five or six. In nearly all Reptiles the tail is well developed. The ribs may have uncinate processes. In many existing forms the sternum, which may be ossified, is rhomboidal, and may have the last pair of ribs attached to a backward median process. Its structure in many fossil groups is not known, but according to Professor Marsh's interpretation some of the Dinosaurs had paired sternal ossifications, corresponding to the two centres from which the sternum develops in the Ratite Birds. Abdominal ribs may be developed in the parietes of the ventral

Fig. 976. — Profile and lateral views of the crown of a tooth of a Dinosaur (*Massospondylus*), with the marginal serrations magnified; from the Mesozoic of India.



A B

Fig. 977.—Posterior (A) and hæmal (B) aspects of a dorsal vertebra of a Snake. The cavities in A on the sides of the neural canal are the zygantra.

surface of the abdomen, and consist of a median and two lateral moieties.

In the pectoral girdle the scapula is generally a more or less elongated bone, with an expansion at its glenoidal extremity. A separately ossified precoracoid exists only in the Anomodonts (fig. 978 *bis*), this bone being in other cases fused either with the scapula, as in the Chelonia (fig. 1008), or with the coracoid, as in Lizards (fig. 830); the fontanelle which frequently occurs in the latter instances apparently marking the original line of separation of the two bones. The coracoid may vary in shape from a long spatulate form (Chelonia) to that of a cheese-cutter (Dinosauria).

The humerus has in many cases no distinct distal condyles (trochleæ), although these are well developed in the Anomodonts, Lizards, and Sphenodon. In the more generalised types there is frequently an entepicondylar foramen to this bone, but in the Lizards and Chelonians the foramen or groove is ectepicondylar; and in a few instances both foramina are present. The radius and ulna always remain distinct. The number of bones in the carpus varies considerably in the different orders, but in *Sphenodon* alone among existing forms is there more than a single centrale; the five distal bones (carpalia) may be all distinct from one another (fig. 829). In the pelvis of the majority of reptiles, the ilium is produced more behind than in front of the acetabulum (fig. 831), and the latter is more or less completely closed by bone; while the pubis (fig. 831) is directed downwards and forwards, and, like the ischium, usually meets its fellow in a ventral symphysis. Among the Dinosaurians, however, the pelvis may be of a Bird-like type, when the pubes do not form a symphysis. Usually the obturator interval forms an open notch; but by the ventral union of the pubis and ischium of the same side this notch may be converted into a foramen. The femur among the Dinosaurs may develop an inner trochanter; and, except in some Ornithosauria, the fibula always remains distinct from the tibia. As in the carpus, the elements of the tarsus vary considerably in the different groups, but the centrale (navicular) is only present in the Anomodontia, the Proterosauria (according to Professor Seeley), one family of Chelonians, and the Ichthyopterygia; while, with the exception of a few extinct types, and perhaps the existing Chelonia, the fourth and fifth tarsalia in all land forms coalesce into a single bone, which supports the fourth and fifth metatarsals. In certain groups—such as the Anomodontia and many of the Chelonia (fig. 829)—the number of phalangeals in the feet of pentedactylate forms may be the same as in Mammals, or 2, 3, 3, 3, 3—the digits being reckoned from the first to the fifth. In Lizards, however, and their allies the number of phalangeals is usually 2, 3, 4, 5, 3 in the manus, and 2, 3, 4, 5, 4 in the pes.

The same numbers obtain in some Dinosauria; but in existing Crocodilia, in which the fifth digit of the pes is aborted, the numbers are 2, 3, 4, 4, 3 and 2, 3, 4, 4. Among the Sauropterygia and in the Ichthyopterygia the number of phalangeals is greatly increased. In a large number of forms the tail is long; but it is generally short in the Anomodontia, Sauropterygia, and Chelonia.

As regards the classification of Reptiles, scarcely any two writers agree as to the number of orders into which the class should be divided, and still less as to their mutual relations, and the larger groups under which these orders may be arranged. There is indeed but little difficulty in regard to existing forms, in which the few orders have become more or less sharply differentiated; but when we go back to the early part of the Mesozoic epoch, we find that nearly all the orders into which the class has been divided show such signs of passing more or less completely into one another, that it is quite impossible to exhibit their true relationship by any system of linear classification. The best arrangement seems, therefore, to group the orders under a series of diverging branches, which will approximate to one another more and more as we recede in time—until, about the epoch of the Lower Permian or possibly the Carboniferous, it is probable that, if we knew all the extinct forms, these branches would be seen to originate either from one, or from but very few parent stems. In regard to the number of these branches, there is still room for a considerable amount of discussion; almost the only absolutely sure ground that we can feel being the association of the three orders forming the Archosaurian branch. To a less extent the same remark applies to the orders themselves; and the right to ordinal distinction of the Proterosauria is not admitted by many writers, while there is not perfect accord in regard to that of the Rhynchocephalia. The provisional arrangement which is adopted in this work is a modification of one recently proposed by Dr G. Baur, of New Haven, and may be tabulated as follows, viz. :—

Theromorous Branch.	Order	1. Anomodontia.
Synaptosaurian "	"	2. Sauropterygia.
	"	3. Chelonia.
Streptostylic "	"	4. Ichthyopterygia.
	"	5. Proterosauria.
	"	6. Rhynchocephalia.
	"	7. Squamata.
Archosaurian "	"	8. Dinosauria.
	"	9. Crocodilia.
	"	10. Ornithosauria.

It may be added that the close approximation to the Amphibia presented by the earlier members of several of these branches

suggests the idea that Reptiles may have been derived from the Amphibians by more than one line of descent.

The Reptiles in the passage of time have suffered more severely than any other class of the Vertebrata, only four of the above-mentioned ordinal groups—viz., the Chelonia, Rhynchocephalia, Squamata, and Crocodilia—now existing; and the second of these being represented only by a single genus with two species. There is some doubt as to the earliest known appearance of the class, since it has been thought that *Mesosaurus* (*Stereosternum*) may be of Carboniferous age, but it is more probably Permian. In undoubted Permian we have the Proterosauria, many of the European Anomodonts, and the Rhynchocephalian genus *Palæohatteria;* while many of the American Anomodontia occur in strata which are referred by the Transatlantic geologists to that period. With the advent of the Trias we find all the orders, with the exception of the Ornithosauria and Squamata, more or less fully represented. And while the former order makes its appearance in the succeeding Lias, we have at present no traces of the latter till the topmost Jurassic. The class reached, however, its zenith of development in the Jurassic and Cretaceous epochs; the greatest number of huge aberrant forms being characteristic of the later part of the former and the earlier part of the latter epoch. Although the one existing Rhynchocephalian genus is closely allied to Triassic forms, yet we have no instance among Reptiles of the existence of a genus right up from that period to the present day, as we have in *Ceratodus* among the Pisces, thus indicating that the higher we ascend in the scale of organisation, the more rapid is the change of types—the same law being exemplified by the occurrence of existing species of Reptiles among the totally extinct Mammals of the Indian Siwaliks.

CHAPTER LIII.

CLASS REPTILIA—continued.

Orders Anomodontia, Sauropterygia, and Chelonia.

Theromorous Branch. — The Reptiles included in this branch or alliance may, for the present at least, be arranged in a single order, although some writers would prefer to regard the suborders into which this order is here divided as of ordinal importance. The most remarkable features found in this order are the resemblance on the one hand to the Labyrinthodont Amphibia, and on the other to the Monotreme Mammals.

Order I. Anomodontia.—This order, which is equivalent to the Theromora (Theromorpha) of Professor Cope, presents the following characteristic features. The body is lacertiform, and the limbs are adapted for walking. The skull is comparatively short, with a fixed quadrate, a parietal foramen, either one or two temporal arcades, and large nasals; in the palate the pterygoids meet together in front of the basisphenoid, which they also join, but diverge anteriorly; while the palatines are generally small, and placed internally to the pterygoids, as in Mammals. When the temporal arcade consists of only a single chain of bones, it is a squamoso-maxillary one (p. 904). The dentition is thecodont, but the teeth may be anchylosed to the bone. The vertebræ have amphicœlous and in some cases notochordal centra; the dorsals carrying long transverse processes, and the ribs articulating by double heads in the anterior region of the trunk. As a rule abdominal ribs appear

Fig. 978.—The palmar aspect of the left humerus of *Ptychosiagum Murrayi*; from the Karoo system of South Africa. Half natural size. *a*, Entepicondylar foramen with the bridge broken away. (After Huxley.)

to be absent. An interclavicle, clavicles, and precoracoids are present, and a sternum was probably always developed. The scapula (fig. 978 *bis*) has an acromial process with which the precoracoid articulates. The humerus (figs. 978, 982), is characterised by its well-developed distal condyles, and the invariable presence of an entepicondylar foramen; while its delto-pectoral crest is generally much developed. In the pelvis the pubis is placed entirely in advance of the ischium, to which it is completely united, with the presence in some forms of a small fontanelle representing the obturator foramen. The ilium may have almost its whole body in advance of the acetabulum. The tarsus has one centrale; and the phalangeals of the manus and pes are typically 2, 3, 3, 3, 3 in number, as in Mammals, the whole structure of the foot being likewise of a Mammalian type.

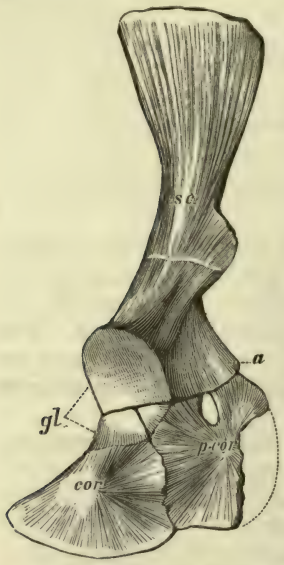


Fig. 978 *bis*.—Lateral aspect of the cartilage bones of the right side of the pectoral girdle of a Dicynodont; from the Karoo system of Africa. *sc*, Scapula; *a*, Acromial process of do.; *p.cor*, Precoracoid; *cor*, coracoid; *gl*, Glenoid cavity. Half natural size.

This order appears to be confined to the Permian and Trias. It has been considered that the Anomodonts are the parent stock not only of all other Reptiles (with the possible exception of the Ichthyopterygia), but also of all Mammals. Later researches do not, however, altogether countenance this view, although there can be no doubt that they are closely allied to the parent stock of Mammals. Recent observations have indeed shown pretty conclusively that this order is directly descended from the Labyrinthodont Amphibians, and more especially from the Archegosaurian family. Thus in the small size or absence of the obturator foramen in the pelvis the entire order shows most decided affinities to that group; while in the small size of the coracoid of some forms, in the presence of a distinct precoracoid (epicoracoid), of very distinct condyles to the humerus, of the centrale in the tarsus, and also in the number of phalangeals, it has characters common both to the Labyrinthodonts and the Monotremes, which are not found together in any other group of Reptiles. These three groups also resemble one another in the non-development, as a general rule, of abdominal ribs; while signs of affinity between them are shown by the shortness of the tail, and the large

size of the exoccipital elements of the occipital condyle in the present order. In the presence of an entepicondylar foramen to the humerus the Anomodonts agree with Rhynchocephalians, Sauropterygians, and Mammals. In many cases (fig. 978 *bis*) the precoracoid forms a large plate-like bone suturally united with the whole of the anterior border of the coracoid, and also articulating largely with the acromial process of the scapula; thus exhibiting a parallelism between the structure of the pectoral and pelvic girdles found in no other reptiles. The above features, together with certain points in the structure of the palate mentioned below, suggest very strongly the descent of the Monotreme Mammals from the same primitive stock as that which gave rise to the Anomodonts. If, moreover, Dr Baur is right in considering that this order does not include the direct ancestors of Mammals, it would appear that the development of its more specialised representatives has followed a course in some respects parallel to that of Mammals.

Suborder 1. Pariasauria.—This suborder includes the most generalised members of the order, which make the nearest approach to the Amphibia. The cranium is at once characterised by the roofing over of its postero-lateral or quadratic region, after the Labyrinthodont manner, by the postorbital, squamosal, and opisthotic bones. Typically the palate, which approximates to an Amphibian type, and has been compared to that of *Nyrania* (fig. 825), apparently has no flooring of the nasal passage to form secondary posterior nares. The skull also has two temporal arcades, and the external surface of the cranial bones is frequently sculptured, as in the typical Labyrinthodonts. The vertebral centra retain a notochordal canal; the number of sacral vertebræ was limited to two, of which only one supports the ilium; and intercentra may be present. The pelvis is of a Labyrinthodont type, the ilium forming a triangular plate elongated in a direction oblique to the axis of the sacrum, with which it articulates obliquely; and there being no obturator foramen between the pubis and ischium. The humerus probably belonging to this group differs from that of other Anomodonts in the slight expansion of the extremities, and in that the lower aperture of the entepicondylar foramen opens on the distal surface of the bone.

Family Pariasauridæ.—The type genus *Pariasaurus* occurs in the Beaufort beds of the Karoo system of South Africa, of which the vertebrate fauna presents a Triassic facies. The best known species (*P. bombidens*) attains the dimensions of a large crocodile; and, with the unfortunate exception of the limbs, the entire skeleton is known, and has been described by Professor Seeley. In addition to the sculpture on the bones of the skull, mucous canals, like those of the Labyrinthodonts, are also present. The teeth are of uniform size, and, although anchylosed to the bone, are set in distinct sockets,

and were replaced after the Crocodilian manner; their crowns being somewhat compressed and grooved. The premaxillæ appear to have been small, as in the Amphibia. There are 29 vertebræ, of which 18 are presacral, and two are anchylosed together to form a sacrum; while wedge-shaped intercentra are also present. The neural spines are extremely short, and the centra of the dorsal vertebræ are very small in proportion to their arches; and only the first sacral vertebra supports the ilia of the pelvis. Small ribs are present in the caudal region; and there was probably a dermal armour.

Professor Seeley concludes that this very remarkable and Amphibian-like Reptile is a direct descendant from the Labyrinthodonts; the chief affinities to that group being displayed in the characters of the skull; in the notochordal canal, and the large arches of the vertebræ; in the support of the pelvis by a single vertebra; as well as in the characters of the pectoral and pelvic girdles. The latter features, together with the general structure of the palate, being identical with those of typical Anomodonts, there appears every reason for referring this family to a suborder of that group.

The genus *Propappus* is founded upon a humerus, from the Karoo system of the Cape, of the above-mentioned type, and there is no direct evidence of its distinctness from *Pariasaurus*. The innominate bone referred to *Dicynodon leoniceps* probably belongs, however, to *Propappus*, which may thus be entitled to stand. The pelvis and sacrum described under the name of *Dicynodon tigriceps* also seem to indicate a member of this suborder, since the ilium is of the same type as in *Pariasaurus*, and is connected with the sacrum by only a single rib, while there is no obturator foramen.

From the general resemblance of its skull to that of *Pariasaurus*, we may refer to this family the genus *Anthodon*, of the South African Karoo system, which, although originally regarded by Sir R. Owen as a Dinosaur, must be included in the present order. It agrees with *Pariasaurus* in the roofing over of the quadratic region, and the continuous replacement of the teeth, which are in a uniform series; but differs in the form of the teeth, which resemble those of the Dinosaurian *Acanthopholis*.

Family Pariotichidæ.—This family, although agreeing with the *Pariasauridæ* in the sculptured cranial bones and the roofing over of the quadratic region, differs in the dentition being of a carnivorous type. All the known genera are from the reputed Permian of North America; and the family is included by Professor Cope in the next suborder. The three genera are *Pariotichus*, *Ectocynodon*, and *Pantylus*. In *Ectocynodon* the first premaxillary tooth is tusk-like, and there is also an enlarged tooth in the middle of the maxil-

lary series. The nostrils are large and lateral; and at the junction of one of the bones of the palate with the maxilla, the tooth-bearing surface is wide, and supports four parallel rows of small obtuse teeth. In *Pantylus*, which was originally described as a Labyrinthodont, the teeth are more equal in size.

Suborder 2. Theriodontia.—This suborder, which is taken (after Dr Baur) to include the Pelycosauria of Professor Cope, is characterised by the absence of a bony roof over the quadratic region of the skull, and the presence of only a single wide temporal arch (fig. 979), apparently consisting of a conjoint squamoso-maxillary and quadrato-maxillary arcade. The mandible has no lateral vacuity.

In some cases, as in the American forms, the vertebræ are still notochordal; intercentra may be developed, to which the capitular heads of the ribs are articulated, and there are not more than two or three sacral vertebræ. The dentition is fully developed. In the palate of the African forms at least the maxillæ develop palatal plates to floor the nasal passage, and thus produce tall and nearly vertical posterior nares, strikingly like those of Mammals. The premaxillæ remain separate.

In those of the typical African forms in which the pelvis is known, the ilium is somewhat intermediate between that of the Pariasauria and Dicynodontia, having a distinct but small obturator foramen. The humerus is usually more or less of a Dicynodont type, having expanded extremities, and the entepicondylar foramen with its lower aperture opening on the palmar aspect of the bone (fig. 982); there is generally a marked thin flange on the postaxial border opposite this foramen which does not occur in the Dicynodonts.

Although evidently nearly related to the Pariasauria the present group departs farther from the Labyrinthodont type, as is shown by the loss of the roofing bones in the quadratic region, as well as of the superior temporal arcade, and by the absence of sculpture or mucous canals on the skull. This advance is also indicated by the development of secondary posterior nares, by the fuller attachment of the ilia to the sacrum, and the relatively larger centra of the vertebræ of the higher types; as well as by the development of the obturator foramen in the pelvis.

Family Tapinocephalidæ.—This family may be taken to include two gigantic Anomodonts from the Karoo system of the Cape, described under the names of *Tapinocephalus* and *Titanosuchus*. The former is known typically by the extremity of the cranium; the vertebræ probably belonging to it having short and notochordal centra. A pelvis, found in association with some limb bones, has been described under the name of *Phocosaurus*, but there is no

evidence to show that it does not belong to *Tapinocephalus*. These associated bones show that the coracoid was distinct from the precoracoid, and that the short and massive humerus had no ectepicondylar foramen. In *Titanosuchus* the dentition (as was probably the case with *Tapinocephalus*) was of a carnivorous type; the humerus is characterised by the presence of an ectepicondylar foramen (in addition to the entepicondylar), which pierced right through the shaft of the bone; while a bone incorrectly described as the pubis shows that the precoracoid was fused with the coracoid.

Family Galesauridæ.—Nearly the whole of the typical Theriodontia of Sir R. Owen may be provisionally included in this family, since, although some genera have single and others double nares, the skulls of the two types so closely resemble one another as apparently to render it impossible to refer them to distinct families. The family is characterised by the humerus (when known) being of a more elongated type than in the preceding family, and by the smaller size of its members; while the vertebræ were probably different from those of the latter, and had no intercentra. The dentition is of a carnivorous type, and differentiated into an anterior, or incisive, series separated by one large tusk or canine-like tooth, from a lateral series of cheek (or molar) teeth; thus simulating the dentition of carnivorous Mammals, and more especially that of the polyprotodont Mesozoic Marsupials. There are no teeth on the palate. The majority of the genera are from the Stormberg and Beaufort beds of the Karoo system of South Africa; and we are mainly indebted for our knowledge of the group to the labours of Sir R. Owen.

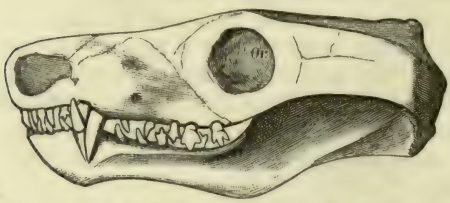


Fig. 979.—Left lateral aspect of the skull of *Galesaurus planiceps*; from the Karoo system of South Africa. Reduced. *Or*, Orbit. Only some of the cheek-teeth are shown.

In the type genus *Galesaurus*, with which *Nythosaurus* is identical, the skull (fig. 979) is much depressed, with the nares divided by a narrow septum; there are 4 anterior and 12 cheek-teeth, the latter having tricuspid crowns. In *Lycosaurus* (fig. 980, A, C) we have larger forms distinguished by the lateral compression of the skull, the distinctly double nares, short mandibular symphysis, and by the number of the cheek-teeth being reduced to 5; the development of the tusks being very great. *Ælurosaurus*, again, appears to be a nearly allied but still more specialised genus, in which, by the reduction of the septum, the nares have united to form a single

opening. *Cynodraco* (fig. 980, B) also includes large forms with greatly developed tusks, having compressed crowns with serrated edges like those of the Mammalian genus *Machærodus;* the nares being divided. Other genera from the Karoo system showing the latter feature are *Cynochampsa*, *Cynosuchus*, and *Scaloposaurus;* the latter being one of the smallest known forms. *Tigrisuchus*, again, is distinguished by its single nares; while *Gorgonops*, of the same deposits, has a narrow flattened skull, with the arrangement of the nares different from that obtaining in all the preceding genera, and

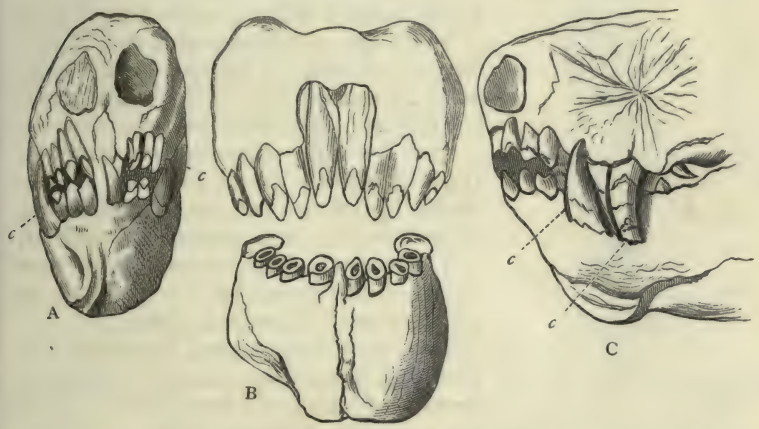


Fig. 980.—A, C, Anterior and lateral views of the skull of *Lycosaurus;* B, Anterior view of the skull of *Cynodraco;* from the Karoo system of South Africa. Reduced. *c* indicates the tusk-like (canine) teeth. (After Owen.)

may indicate a distinct family. *Deuterosaurus* and other forms from the Permian of Russia, which are included by Sir R. Owen in the typical Theriodontia, are noticed below.

Family Clepsydropidæ.—This name is applied by Professor Cope to carnivorous Theriodontia, distinguished from the *Galesauridæ* either by the development of teeth on the palate, or by the extraordinary character of their dorsal vertebræ, in which large intercentra are typically present. All the genera are typically from the reputed Permian deposits of North America. In the type genus *Clepsydrops* the premaxillary and maxillary teeth are of unequal size, and the dentary bone of the mandible has two enlarged tusks near its extremity. Teeth are also borne on the pterygoids; and the neural spines of the dorsal vertebræ are not excessively elongated. In *Dimetrodon*, the most remarkable character is the extraordinary development of the neural spines of the dorsal vertebræ, which resembled those of *Naosaurus* (fig. 981),

with the exception of having no horizontal processes. The height of the spine in one species is more than twenty times the length of the centrum; and Professor Cope concludes that these spines formed a kind of elevated fin on the back, of which it is difficult to imagine the use. *Naosaurus* differs from the preceding by the above-mentioned horizontal processes on the spines of the vertebræ (fig. 981). The premaxilla had one tusk; and there were two similarly enlarged teeth near the anterior extremity of the maxilla, behind which comes a series of some twelve teeth of equal size, with compressed and slightly recurved crowns. Numerous small obtuse teeth are also dotted over the palatines and pterygoids. This genus has also been recorded from the Permian of Bohemia. Other American genera included in this family by its founder are *Embolophorus*, *Edaphosaurus*, *Archæobelus*, *Theropleura*, and perhaps *Lysorophus* — *Theropleura* being characterised by the presence of well-developed abdominal ribs.

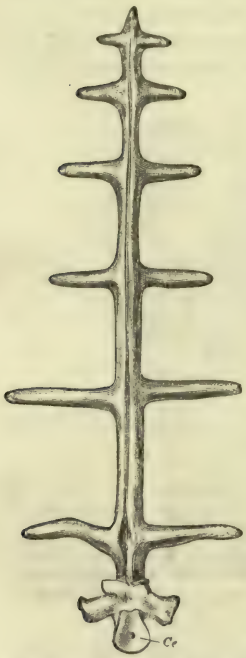


Fig. 981.—Anterior view of dorsal vertebra of *Naosaurus claviger*; from the Permian of Texas. One-sixth natural size. *Ce*, Centrum. (After Cope.)

Here may be mentioned the genus *Stereorhachis*, from the Lower Permian of France, of which the lateral cheek-dentition presents a considerable resemblance to that of *Naosaurus*, although it is not known whether teeth were present on the palate. The neural spines of the vertebræ are of normal type; but it is not known whether intercentra were present, or whether the centra were notochordal. The humerus (fig. 982) differs from that of the *Galesauridæ* in the contour of the distal extremity. Professor Seeley regards the above-mentioned humerus from the Karoo system of the Cape, described by him under the name of *Propappus*, as indicating an allied form, but there is nothing to justify this association. *Stereorhachis* may constitute the type of a distinct family, but there is at present no evidence to support the view that this genus (together with *Propappus*) represents a distinct order, for which the name Gennetotheria has been proposed.

Family Bolosauridæ.—This family is also typically known from the reputed Permian of North America, where it is represented by the genera *Bolosaurus* and *Chilonyx*. In the former, the teeth are fixed in shallow alveoli, and have their crowns ex-

panded transversely to the axis of the jaws. These crowns are swollen at their base, and have a low apex vertically divided into two portions, of which the inner one in the upper jaw is low and horizontal, and the outer forms a curved claw-like cusp — the anterior teeth consisting simply of an inner ledge and the outer cusp, and there being no enlarged tusks. *Metarmosaurus*, of the same deposits, may perhaps be referable to this family.

In the large *Deuterosaurus*, from the Russian Permian, the premaxillary teeth (fig. 983) approximate to the description of those of *Bolosaurus*, but there are large tusk-like teeth resembling those of the *Galesauridæ* behind the five premaxillary teeth; the nares being divided. This genus may be regarded as representing a distinct carnivorous family. A tooth from the Karoo system of South Africa, having the general characters of the anterior teeth of *Deuterosaurus*, but with the lateral borders of the inner surface of the crown forming ridges, has been made the type of the genus *Glaridodon*. An associated series of bones in the British Museum may belong to the same form; the vertebræ are notochordal, and the humerus agrees in size with the one mentioned below as *Brithopus*. Here may be noticed the genus *Rhopalodon*, from the Permian of Russia, founded upon a mandibular ramus which may belong to the same family. Perhaps, however, the most remarkable specimen from these deposits is the distal portion of a large humerus described under the name *Brithopus* (*Eurosaurus*); the proximal end of another humerus, which has received the name of *Orthopus*, probably belonging to the same species. The former specimen is remarkable for having both ectepicondylar and entepicondylar foramina—a condition elsewhere known only in *Titanosuchus* and *Sphenodon*. Dr Baur has suggested that this specimen may belong to a Rhynchocephalian, but it is certain that it is referable, as Sir R. Owen first pointed out, to the present suborder; and it is quite likely that it may prove to belong to *Deuterosaurus*, in which case this name should be superseded.

Fig. 982.—Anterior aspect of the imperfect left humerus of *Stereorhachis dominans*; from the Lower Permian of France. One-half natural size. (After Gaudry.)

Family Diadectidæ.—This family is also founded upon genera

from the Permian of North America, and includes *Diadectes*, *Empedias* (*Empedocles*), and *Helodectes*. The teeth (fig. 984) are transversely elongated like those of *Bolosaurus*, and are also divided by a median vertical ridge; but both the inner and the outer moieties are equally low. Their alveoli are not separated, and the edges of the crowns are obtuse, with tuberosities on some of them distinct from the apex of the main ridge. Professor Cope regards this peculiar type of dentition as indicative of a herbivorous diet. The brain-case differs from that of the *Clepsydropidæ* in a manner analogous to that in which the brain-case of the *Varanidæ*

Fig. 983.—Lateral view of a premaxillary tooth of *Deuterosaurus biarmicus*; from the Upper Permian of Russia. Half natural size.

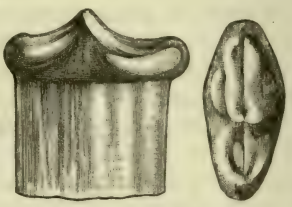


Fig. 984.—Lateral and palatal view of a posterior tooth of *Empedias molaris*: from the Permian of North America.

is distinguished from the same part in other Lacertilia—that is, it is continued between the orbits so as to enclose the olfactory lobes in bone. *Phanerosaurus*, from the Permian of Germany, is referred by Professor Cope, from the structure of its vertebræ, to this or the preceding family.

Suborder 3. Dicynodontia.—In this suborder the vertebræ have no notochordal canal; intercentra are wanting; and the sacrum includes from four to five vertebræ. There is in no case more than one pair of teeth in the alveolar borders of the upper jaw, while there are none in those of the mandible. The palate is of the general type of that of the Theriodonts, but the premaxillæ unite to form a single beak-like bone, and the mandibular symphysis, which is very deep and laterally compressed, is likewise anchylosed. The nares are double; and it is probable that in some forms a part or the whole of the alveolar borders of the mandible was sheathed in horn; while the mandibular rami have lateral vacuities (fig. 985, B). There is a single temporal arcade, which appears to be a squamoso-maxillary one. In the pelvis the ilium is much expanded in an antero-posterior direction, the expanded plate

lying nearly parallel to the sacrum; and there is a small obturator foramen. The humerus (fig. 978) is expanded at the two extremities, with a prominent deltopectoral crest,[1] and with the lower aperture of the entepicondylar foramen opening on to the palmar aspect. The members of this group are found in the Stormberg and Beaufort beds of the Karoo system of South Africa, and the equivalent Gondwanas of Central India.

Family Dicynodontidæ.—This family is characterised by the absence of teeth on the palate. The type genus *Dicynodon* was the first known representative of the order, and was originally described by Sir R. Owen from specimens brought from South

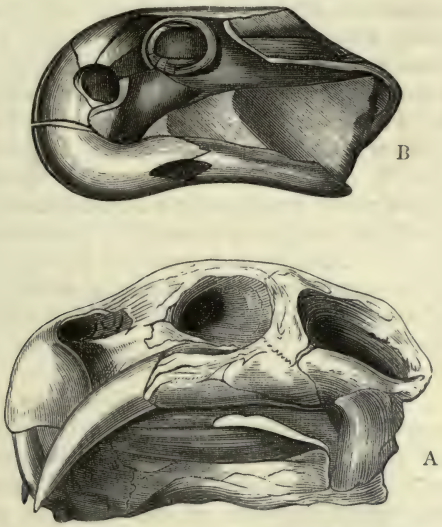


Fig. 985.—Lateral view of the skull of (A) *Dicynodon lacerticeps*, and (B) *Udenodon Baini*; from the Karoo system of South Africa. Reduced. (After Owen.)

Africa. It is characterised by the presence of a tusk-like tooth (fig. 985, A) growing from a persistent pulp in each maxilla—the rest of the jaws being edentulous, with trenchant edges. The profile of the skull is rounded, the maxillæ are not strongly ridged, the nares are approximated to the muzzle, and the supraoccipital forms a broad bar above the foramen magnum. This genus may also occur in the Panchet stage of the Indian Gondwanas. In *D. tigriceps* the skull has a length of 20 inches. In *Ptychosiagum*[2]

[1] The deltopectoral crest is the ridge on the right side of the upper half of the figure.

[2] This new name is proposed in lieu of *Ptychognathus*, which is preoccupied.

(*Ptychognathus*) there is also a pair of tusk-like upper teeth, but the skull is angulated, with strong ridges on the maxilla, the nares far behind the muzzle, and only a very narrow supraoccipital bar above the foramen magnum. The typical species are from South Africa, but another representative of the genus occurs in the Gondwanas of Central India, which was originally described as *Dicynodon orientalis*. A very imperfect and flattened skeleton from the Karoo system has been made the type of the genus *Cirognathus*, which is said to be characterised by the small size of the canine-like tooth, and the presence of only two phalangeals in all the digits except the third. It appears, however, that these alleged differences do not really exist, the difference in the humerus being due to a comparison of opposite aspects, and the number of phalangeals being apparently normal, so that this form probably belongs to *Dicynodon*. The same remark will apply to part of a skeleton from the same beds upon which the genus *Eurycarpus* has been founded. The genus *Udenodon* (*Oudenodon*) is characterised by the total absence of teeth (fig. 985, B), but is otherwise so closely allied to *Dicynodon* that it must certainly be included in the same family. The nares are somewhat approximated to the orbits, and the profile of the muzzle is rounded. It occurs in the Karoo system of the Cape Colony; and some of its representatives attained very large dimensions. *Cistecephalus* (*Kistecephalus*) comprises smaller forms from the same beds, in which the skull is much depressed, with the orbits directed frontally. There was a pair of tusks in the maxillæ.

The name *Platypodosaurus* has been applied to a considerable portion of the skeleton of a Dicynodont, from the Karoo system, of which the skull is unfortunately unknown, and which may prove to be identical with *Udenodon*, unless it belong to *Endothiodon*. The remarkably Mammalian structure of the pelvis, in which there is a small obturator foramen between the pubis and the ischium, is fully noticed in Sir R. Owen's description of the specimens.

Family Endothiodontidæ.—The remarkable genus *Endothiodon*, comprising large reptiles from the Karoo system of the Cape, forms the type of a family distinguished from the preceding by the presence of teeth on the palate. The skull presents a strong general resemblance to that of *Udenodon*, but the muzzle is more elongated, and the nares are terminal and overhung by the massive nasals. The alveolar borders of the jaws are trenchant, but the oral surface of the palate and mandible carry one or more longitudinal rows of columnar and cylindrical teeth. The remarkably Mammalian type of the palate of *Endothiodon* is noteworthy. The skull from the same deposits described as *Theriognathus* seems to belong to *Endothiodon*.

Endothiodon has been compared to the Rhynchocephalian *Rhynchosauridæ* and also to *Placodus;* but although there is a marked superficial resemblance between the three forms in the palate and teeth, yet this resemblance is but apparent, since while in *Endothiodon* the teeth are borne on a secondary bony floor beneath the narial passage, in the other genera they are supported on the proper surface of the palate, on which the posterior nares open directly, without the intervention of a secondary passage.

Suborder 4. Procolophonia.—According to a recent observer the genus *Procolophon*, represented by comparatively small forms from the Karoo system of the Cape, differs so decidedly from the Theriodontia that it is entitled to form a distinct suborder, showing marked signs of affinity with the Rhynchocephalia. The *Procolophonidæ* have a full dentition, but no tusk-like teeth, and the nares are double. Although the pectoral girdle still has a distinct precoracoid, yet its whole characters approximate to those of the Rhynchocephalian genus *Sphenodon.* The humerus also resembles the corresponding bone of the latter; and in the skull the pterygoids extend forwards in the same manner to join the vomers and exclude the palatines from the middle line; while there are no secondary posterior nares; and teeth are borne on both the pterygoids and vomers, as in the young of *Sphenodon.*

Group Placodontia.—Our sole knowledge of this group, represented by *Placodus* (fig. 986) and *Cyamodus* of the Middle Trias, or Muschelkalk of Germany, is derived from the skull, so that we are at present to a great extent in the dark as to their true affinities. These forms, after having been regarded as Ganoid Fishes, were referred by Sir R. Owen to the Sauropterygia; and the type genus resembles the Nothosaurs in the backward position of the nares and the form of the cranial rostrum. The skull has, indeed, been said to present many points of resemblance to that of the Anomodonts, and more especially *Endothiodon*, to which genus it is considered by Sir R. Owen to be closely allied. The resemblance in the form of the palate is, however, as already mentioned, only a superficial one; the present form having no floor to the narial passage, and the posterior nares opening directly into the roof of the mouth by horizontal apertures, as in the Sauropterygia. The skull is broad posteriorly, with double nares, a deep and apparently compound temporal

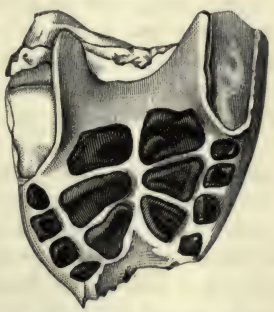


Fig. 986.—The imperfect palate of *Placodus gigas;* from the Muschelkalk of Bayreuth. One-fourth natural size. When entire the muzzle would form a produced rostrum.

arcade, and a postorbital bar. The palatal teeth (fig. 986) resemble paving-stones, and were probably adapted for crushing hard substances like the shells of Molluscs. In the upper jaw the teeth are arranged in an outer or maxillary series of small ones, and an inner or palatine series of larger ones; all being implanted in shallow sockets and replaced by vertical successors. In the mandible there is but one row of teeth. The number of palatal teeth varies in the different forms; and there are also modifications in the size and contour of these teeth, which aid in affording generic and specific characters. The premaxillary teeth may be of a more or less prehensile type. Till the vertebræ and limb-bones are known the position of these forms must remain uncertain; but it may be remarked that all the known limb-bones from the Muschelkalk, except those of Dinosauria, appear to be of a Sauropterygian type.

In the typical genus *Placodus* the skull is comparatively narrow, and has a long rostrum produced considerably in advance of the nares. The palatal teeth (fig. 986) have polygonal crowns, those of the palatine series being three in number on either side, and closely approximated; while the three premaxillary teeth are more or less chisel-like, and are separated by an interval from those on the palate. The mandible has a long symphysis, and two pairs of cutting-teeth. The maxillary teeth may be either four or five on either side. *Cyamodus* is readily distinguished by the great width and shortness of the cranium, which has no distinct rostrum, with the nares placed at the muzzle and the premaxillæ fused together. The palatal teeth have rounded crowns, the crown of the last palatine being very large; there may be either two palatine and three maxillary, or two maxillary and three palatine teeth. There were but two pairs of premaxillary teeth, which are not chisel-like. In the lower jaw the symphysis was triangular and comparatively short, and was probably devoid of teeth.

Recently Dr Gürich has proposed the name *Pleurodus* for an allied form from the Muschelkalk of Silesia, but since this term is preoccupied for a Crocodilian genus it will have to be changed.

Synaptosaurian Branch.—According to Dr Baur's scheme of classification this branch comprises the orders Sauropterygia and Chelonia; although Professor Cope and Mr Boulenger would also include the Rhynchocephalia. The typical Proganosauria of Dr Baur may be merged in the Sauropterygia. Although the Sauropterygia and Chelonia present many characters in common, yet it is not easy to give a definition of this branch. In all, however, the quadrate is firmly united to the skull; and all, or nearly all, of the dorsal ribs articulate with the vertebræ by single heads. As a general rule the palate is more or less completely closed, the pterygoids generally extending forwards to join the vomers. There may be

either one or two temporal arcades. A parietal foramen is present at least in the young. In all cases ossifications are developed upon the ventral aspect of the body, either in the form of abdominal ribs, or of a plastron; but there are none in the sclerotic of the eye. The sacral ribs are connected with the vertebræ by upper and lower articulations; and when chevrons are present they are mainly or exclusively attached to the hinder borders of the caudal centra. A precoracoid anchylosing to the scapula may be present in the pectoral girdle; and in the pelvis the pubis and ischium have expanded and flattened ventral surfaces, and the obturator foramen may be completed by the union of the ischium with the pubis of the same side. There is, moreover, a considerable structural resemblance between the limb-bones of the more generalised forms of the two orders, these bones always having terminal epiphyses; and the tarsus in both may be of a very primitive type. The humerus may have either an entepicondylar (ulnar) foramen and an ectepicondylar (radial) groove, or only the latter, or may be devoid of both. The ribs never have uncinate processes.

We are still very much in the dark as to the origin of these two orders, although the Sauropterygia can be traced back to a form presenting several Amphibian features, which appears to have been closely allied to the primitive Rhynchocephalians. From the disappearance of numerous segments in the vertebral column of the Chelonia during development, Professor Parker has suggested that this order has originated from a type allied to the Sauropterygia; and their plastron is almost certainly derived from, or developed upon, the abdominal ribs of a form allied either to the Rhynchocephalia or to *Mesosaurus*.

Order II. Sauropterygia.—In this extinct order the body was devoid of any exoskeleton, while the neck was more or less elongated, and the tail short. In the skull there is only the superior temporal arcade; the narial apertures are lateral and more or less approximated to the orbits; the premaxillæ are very large; and there is a well-developed parietal foramen in the adult. The prefrontal remains distinct; the postorbital may be separate from the postfrontal; typically there is a transverse bone; and the symphysis of the mandible is united by suture. The teeth, which are implanted in distinct sockets and confined to the margins of the jaws,[1] have curved sharp crowns, with fluted enamel. Each rib articulates to a single vertebra, and in the cervical region the costal facets, which may be either single or double, are situated entirely on the centrum, and generally are not prominent. The vertebræ are amphicœlous; and the neuro-central suture may be either persistent throughout

[1] Assuming that the Placodontia are distinct from this order.

life, or completely obliterated. All those vertebræ in which the costal articulation is on the centrum below the neuro-central suture may be reckoned as cervical; their number varying from about 21 to nearly 40. The centrum of the atlas is well developed, and there is a wedge-shaped intercentrum between the latter and the skull. The true cervicals are succeeded by a few vertebræ in which the costal articulation is partly on the arch and partly on the centrum, for which the name of pectorals has been proposed. The dorsal vertebræ have the costal articulation placed entirely on the arch, and generally forming an elongated transverse process. The caudal vertebræ are always furnished with true ribs, and also with chevron-bones, which may not be united below. The structure of the pectoral girdle is very remarkable, and has given rise to considerable diversity of opinion. In all forms the coracoids meet in a median symphysis, which may be short (fig. 987) or very long (fig. 988).

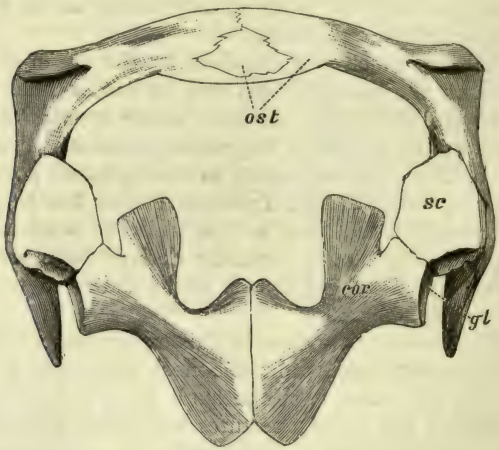


Fig. 987.—Ventral aspect of the pectoral girdle of *Nothosaurus mirabilis*; from the Muschelkalk of Würtemberg. Reduced. *ost*, Clavicle and interclavicles; *sc*, Scapula; *gl*, Glenoid cavity; *cor*, Coracoid.

In the generalised *Nothosaurus* (fig. 987) the scapula has only a small ventral portion, separated by a wide interval from that of its fellow. Anteriorly to these ventral plates of the scapulæ there is a slender arch consisting of a median and two lateral portions, corresponding to a similarly situated bone in *Plesiosaurus*. This arch is usually correlated with the interclavicle and clavicles; but from the deep-seated position of its representative in *Plesiosaurus*, Mr Hulke considers that in that genus it corresponds to the omosternum of the Amphibia, and if this interpre-

tation be correct, it will have the same homology in *Nothosaurus*.[1] As specialisation proceeds it appears that the scapulæ have tended to develop very large ventral plates, with a concomitant reduction and ultimate disappearance of the clavicular arch. The intermediate stage is shown in *Plesiosaurus* (fig. 997), where it will be seen that the ventral plates of the scapulæ are separated in the median line; and the culmination in *Cimoliosaurus*, where they unite in a median symphysis, and join the anterior extremities of the coracoids, while the interclavicle has disappeared. Mr Hulke regards the ventral plate of the scapula as representing the precoracoid of the Chelonia, but further evidence is required to prove this; the view that it represents the clavicle being obviously incorrect. In the pelvis the pubis usually forms a wide plate, while the ischium is somewhat chopper-shaped; in some cases the pubis and ischium of each side unite to enclose an obturator foramen. The ischia are strikingly like those of the Amphibia, and have a long symphysis. The limbs are subject to considerable variation; those of the earlier generalised forms being adapted for progression on land, while in the specialised types they are modified into paddles. In all cases, however, the limbs are readily distinguished from those of the Ichthyopterygia by the relatively longer humerus and femur, and the absence of interdigital bones. The limb-bones are regarded by Professor Seeley as showing signs of Amphibian affinity. A peculiar feature in the limb-bones is that the epiphyses (fig. 989) of the humerus and femur are enormously developed, and form large cones at either extremity of the bones, almost, or completely, meeting in the middle of the shaft, which is reduced to a pair of elongated cups. The bones of the palate

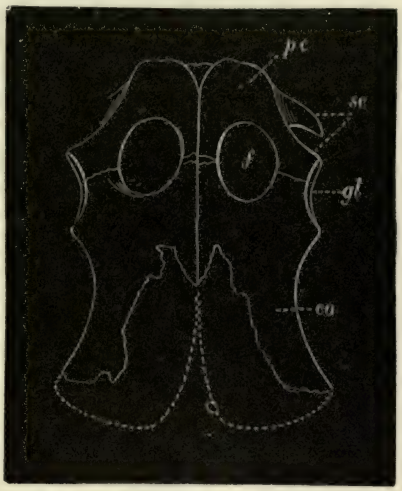


Fig. 988.—Ventral aspect of the pectoral girdle of *Cimoliosaurus* (*cf*) *trochanterius*; from the Kimeridge Clay. Reduced. *sc*, Scapula; *pc*, Ventral (precoracoidal) plate of do.; *gl*, Glenoid cavity; *f*, Scapular foramen; *co*, Coracoid. (After Hulke.)

[1] In the British Museum Catalogue of Fossil Reptilia Mr Hulke's interpretation of the homology of these bones was provisionally adopted, but the writer now considers that the other interpretation is probably the true one.

never develop plates to form a floor to the nasal passage, so that the posterior nares also open directly into the mouth by horizontal apertures (fig. 991).

This order ranges in time probably from the Permian and certainly from the Trias to the Upper Chalk, and we are enabled to trace the gradual evolution of the specialised marine forms from those less widely separated from a normal type. All these reptiles appear to have been carnivorous.

Family Mesosauridæ—The genus *Mesosaurus*, originally described from the Karoo system of Griqualand in South Africa, which is probably of lower Mesozoic age, but subsequently found in beds of uncertain age in Brazil, and described under the name of *Stereosternum*, includes small reptiles regarded by Dr Baur as

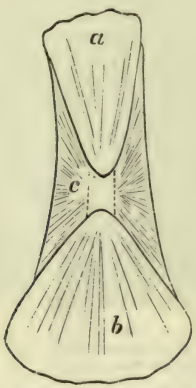


Fig. 989.—Longitudinal section of a Sauropterygian humerus; from the Kimeridge Clay; one-sixth natural size. *a*, Proximal, *b*, Distal epiphysis; *c*, Shaft.

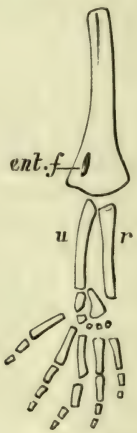


Fig. 990.—Ventral aspect of the left pectoral limb of *Mesosaurus tenuidens;* from the Karoo system of Griqualand. *ent.f*, Entepicondylar foramen of humerus; *r*, Radius; *u*, Ulna.

constituting a distinct order — the Proganosauria, — but which appear to be so closely related to the *Nothosauridæ*, that there can be little, if any, hesitation in including them in the same order. The Brazilian form was originally referred with some hesitation by Professor Cope to the Amphibia. One of the most peculiar features of this genus, in which it differs from all other groups except the Amphibia, the extinct *Palæohatteria*,[1] and perhaps the Chelonia is the separation of the fourth and fifth tarsalia, so that each metatarsal articulates with a distinct tarsale. The centra of the vertebræ

[1] See Rhynchocephalia, *infra*.

have a small notochordal canal, and are small in comparison to the neural arches; while the ribs seem to have been anchylosed to the vertebræ, and were of great thickness, like those of the next family. The system of abdominal ribs was strongly developed. The skull is much elongated, and has slender recurved teeth, which were in all probability implanted in distinct alveoli. The pectoral girdle appears to be very similar to that of the *Nothosauridæ*, the presumed interclavicle not being T-shaped; and a similar close resemblance is presented by the pectoral limb (fig. 990), in which the humerus has an entepicondylar, or ulnar, foramen, like that of Mammals. The pelvis is considered to have had only a very small obturator foramen; the ischia and pubes forming broad expanded plates like those of Amphibia and other Sauropterygia. The terminal digits were devoid of claws; and the feet were probably webbed like those of frogs.

Dr Baur makes this genus the type of the order Proganosauria, in which he would also include the undermentioned genus *Palæohatteria;* and regards this order as the connecting-link between Amphibians and Reptiles. Although there is something to be said in favour of this view, yet the manifest affinity of *Mesosaurus* to the more typical Sauropterygia, and of *Palæohatteria* to the Rhyncho-

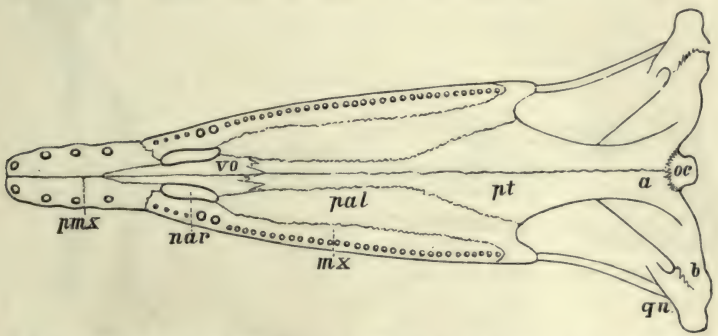


Fig. 991.—Palatal aspect of the cranium of *Nothosaurus mirabilis;* from the Muschelkalk. One-eighth natural size. *pmx*, Premaxilla; *nar*, Posterior nares; *vo*, Vomer; *mx*, Maxilla; *pal*, Palatine; *pt*, Pterygoid; *a*, Ala of do.; *b*, Quadratic ridge of same; *qu*, Quadrate; *oc*, Occipital condyle. The posterior extremity of *pal* is probably formed by a distinct transverse bone.

cephalia, seem to render it more advisable to refer those genera to the two orders in question, of which they will respectively form the most generalised stage. By this arrangement the intimate connection of both orders with the Amphibia will be made manifest.

Family Nothosauridæ.—In this family, which comprises some forms of large size, the limbs were furnished with claws, and adapted to a certain extent for walking. In the skull the pterygoids either

diverged posteriorly, or gave off wings uniting in the middle line upon the basi- and presphenoid, and thus completely closing the posterior portion of the palate (fig. 991)—an approximation to the latter arrangement occurring in some Chelonia. The palate was also devoid of infraorbital vacuities. The coracoids (fig. 987) had a short median symphysis, not extending as far forwards as the scapular articulation, and also had a groove; while the ventral plates of the scapulæ were very small. Typically, the cervical vertebræ have double costal facets, while the transverse processes of the dorsals are very short, and remarkable for the vertical elongation of their articular faces. The humerus and femur are elongated —the former (fig. 993) having an entepicondylar foramen, but no distinct distal expansion. The ischium and pubis did not unite to enclose an obturator foramen.

The known forms occur typically in the Muschelkalk, or Middle Trias, of the Continent, but some of them range up into the overlying Keuper, and one species is found in the Bunter, or Lower Trias. In the typical genus *Nothosaurus* the skull (figs. 991, 992) is long and much depressed, the length of the post-orbital exceeding that of the preorbital portion. The characters

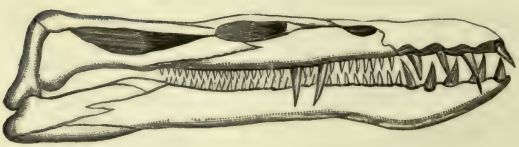


Fig. 992.—Right lateral aspect of the skull of *Nothosaurus mirabilis*. Reduced. (After Meyer.)

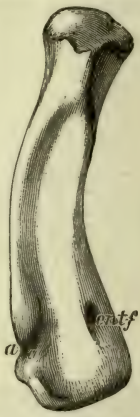


Fig. 993.—Ventral aspect of the right humerus of *Conchiosaurus*. One-half natural size. *Entf*, Entepicondylar foramen; *a*, Ectepicondylar groove.

of the palate are shown in fig. 991. *Conchiosaurus* is a closely allied but smaller form, in which the teeth are club-shaped. In *Simosaurus* the skull is characterised by the breadth of the facial portion and its stout teeth. The type species is nearly equal in dimensions to the larger species of *Nothosaurus*. Finally, *Pisto-*

saurus is distinguished by the posterior divergence of the pterygoids, and not improbably by the presence of long transverse processes to the dorsal vertebræ; both of these features being Plesiosaurian. The preorbital portion of the skull is very narrow. Although the members of this family have lost all traces of a notochordal canal in the centra of the vertebræ, yet the ossification of these centra has taken place in the same manner by means of a sheath investing the notochord.

Family Lariosauridæ.—This family is closely allied to the preceding, but the limbs approximate to those of the *Plesiosauridæ*. The skull, at least in one genus, has infraorbital vacuities on the palate, and the coracoid has no notch at its glenoidal extremity. The femur always remains an elongated bone, longer than the epipodials and metapodials collectively; but the humerus may be comparatively short, and is more or less expanded at its distal extremity; while in *Lariosaurus*, although not in the other forms, it has lost its foramen. The terminal phalangeals of the pes still retain their claws. In *Neusticosaurus* it is thought that cervical ribs were wanting. The type genus *Lariosaurus* comprises one medium-sized species from the Trias of Lombardy, and according to Dr Baur, has both limbs adapted for walking. The palate is unknown. In *Neusticosaurus*, from the Lettenkohle at the base of the Keuper of Würtemberg, Professor Seeley considers that the pectoral limb had become modified into a paddle, although this conclusion is not accepted by Dr Baur. It appears probable that a small reptile, described from the Trias of Italy under the preoccupied name of *Pachypleura*, is not more than specifically separable from *Neusticosaurus*. The type species of the latter was about one foot in length, and was probably of amphibious habits.

It may be convenient to notice here two small Triassic reptiles which are referred by Dr Baur to this family, although Dr Deecke considers that at least the second has more affinity with the Lizards. These genera are *Dactylosaurus*, from the Muschelkalk of Silesia, and *Macromerosaurus*, from the Italian Trias; the former being almost certainly referable to this order, and perhaps not separable from *Neusticosaurus*. In this connection it should be observed that Dr Bassani considers *Macromerosaurus* to be identical with the type species of *Lariosaurus*, and that *Neusticosaurus* is not generically separable from the latter. *Pachypleura* is, however, regarded as distinct from *Neusticosaurus*, in which case it will require a new name, as the present one is preoccupied.

Finally, it should also be mentioned that some authorities would regard the two preceding families as constituting a distinct suborder—the Nothosauria—but the transition to the next family is almost complete.

Family Plesiosauridæ.—With this group we come to the consideration of the typical members of the order, all of which were adapted for a purely aquatic life, and probably frequented coasts and estuaries. In the skull the pterygoids diverge posteriorly, and do not overlie the basisphenoid; while there were small infraorbital vacuities in the palate. The dorsal vertebræ have long transverse processes. In the pectoral girdle the scapulæ have large ventral plates, which may meet in the middle line; and the symphysis of the coracoids is much elongated, and extends in advance of the scapular articulation. In the limbs (fig. 994) the humerus and femur were comparatively short and distally expanded; the former being devoid of a foramen. The bones of the second segment are likewise very short, and strangely altered from the normal form. In certain cases, moreover, a third bone (fig. 998) articulates with the humerus and femur, of which the homology will be discussed under the head of the Ichthyopterygia. The metacarpals and phalangeals are, however, still elongated, but the number of the latter is increased beyond the normal complement. Further, the terminal claws have disappeared; and the whole limbs were doubtless enveloped in a common integument, to form paddles after the fashion of the turtles. The coracoid (fig. 988) is remarkable for its great

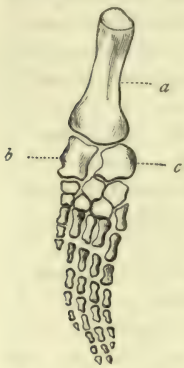


Fig. 994.—Dorsal aspect of the left pectoral limb of *Plesiosaurus Hawkinsi*; from the Lower Lias of Dorsetshire. Reduced. *a*, Humerus; *b*, Radius; *c*, Ulna.

Fig. 995.—Skeleton of *Plesiosaurus dolichodirus*; from the Lower Lias. Greatly reduced. (After Conybeare.)

antero-posterior length, and has no fontanelle. This family includes some forms of huge dimensions; its range extending from the Rhætic, or Uppermost Trias, to the Chalk.

The *Plesiosauridæ*, like the Crocodiles of the present day, differ greatly among themselves in the relative length of the mandibular symphysis, as is shown in the accompanying woodcut. In the present family it appears, however, that the result of evolution and specialisation has been towards the gradual lengthening of this sym-

physis; whereas among the Crocodilia the tendency has been precisely in the opposite direction.

This family has been divided into a large number of genera, but since several of these are not really distinct it will suffice to adopt a smaller number of such divisions. The genus *Plesiosaurus*, as now restricted, is exclusively confined to the Upper Trias (Rhætic) and Lias. Owing to the beautiful preservation of many of the species

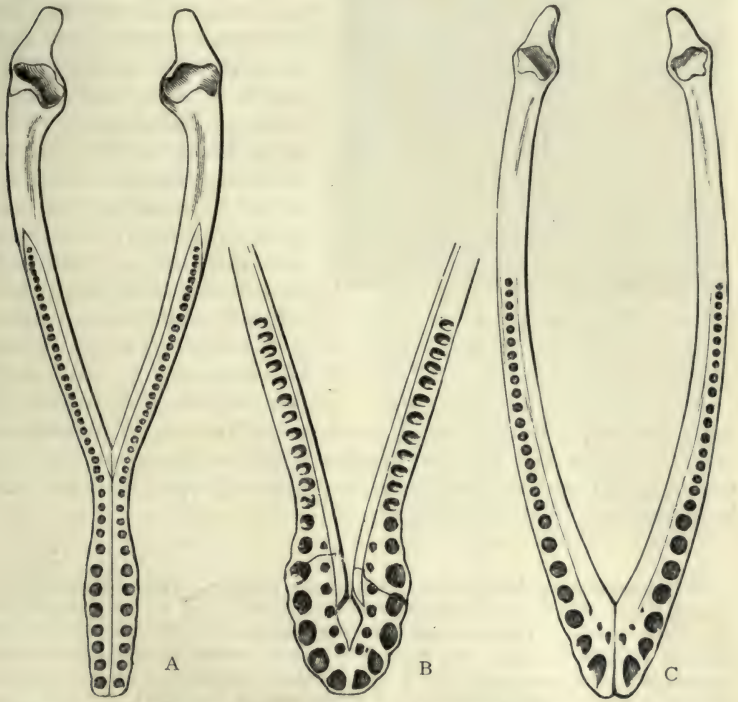


Fig. 996.—The mandible in different genera of *Plesiosauridæ*. Reduced. A, *Peloneustes philarchus*, from the Oxford Clay, one-eighth natural size: B, *Thaumatosaurus indicus*, from the Upper Jurassic of India, one-seventh natural size; C, *Plesiosaurus dolichodirus*, two-fifths natural size.

this genus has been long known to science; and its remains were admirably described in the first third of the present century by the late Mr Conybeare and Dean Buckland, who with remarkable foresight hinted at the affinity of these strange and weird forms of Reptilian life to the Chelonia. In this genus the skull is either small with a short mandibular symphysis (as in fig. 996, C), or moderately large with a longer symphysis and rostrum. The teeth are generally slender, without carinæ, and the terminal ones are not much larger

than the others in the more typical species. The neck is more or less elongated, with the anterior vertebræ in most cases very small. The cervical ribs and neural arches are firmly articulated to the centra of the vertebræ, but traces of the suture usually persist; in the cervical region the facets for the articulation of the ribs are usually double, and the terminal faces of the centra generally ellipsoidal, and more or less cupped. The most characteristic features of the genus are, however, to be found in the pectoral girdle (fig. 997), in which the scapulæ are relatively small, and widely separated in the middle line, where they rest upon the interclavicle, with its small and deep notch. The coracoids are, moreover, long and rather narrow, with a median production in advance of the glenoid cavity; while the foramen between the coracoid and scapula is very large and open towards the interclavicle.

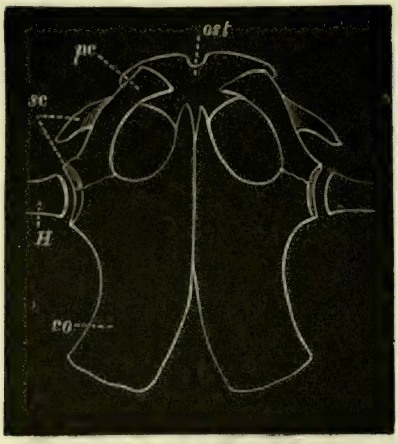


Fig. 997.—Ventral aspect of the pectoral girdle of *Plesiosaurus dolichodirus*; from the Lower Lias of Dorsetshire. Reduced. *ost*, Interclavicle; *sc*, Scapula; *pc*, Ventral plate of do.; *co*, Coracoid; *H*, Head of humerus. (After Hulke.)

This genus may be divided into three groups. The *Longirostrine* group, represented by *P. rostratus* of the Lower and *P. longirostris* of the Upper Lias, is characterised by the comparatively elongated mandibular symphysis, and the extremely short neural spines and single costal facets of the majority of the cervical vertebræ. In the typical group we have *P. dolichodirus* with its extremely long neck (fig. 995), the shorter-necked *P. Hawkinsi*, and the large *P. Conybeari*, all being from the Lower Lias. These forms have a moderately short mandibular symphysis (fig. 996, c), while the centra of the cervical vertebræ are never greatly elongated, and there are double costal facets and moderately tall neural spines in this part of the vertebral column. The third group is represented only by *P. homalospondylus*, of the Upper Lias, which is characterised by the great elongation of the centra of the cervical vertebræ, which have flat terminal faces, and enormously tall neural spines. The resemblance of these vertebræ to those of the cervicals of the typical group of the Jurassic and Cretaceous genus *Cimoliosaurus* suggests the origin of the latter group from the present; whereas on similar grounds it may be suggested that the *Cœlospondyline* group of *Cimoliosaurus* has originated from the typical group of *Plesiosaurus*. In all species of the present genus the radius and ulna (fig. 994) still retain evidence of their

original character as long bones, and are separated by a well-marked interval.

Another exclusively Liassic and perhaps Rhætic genus is *Eretmosaurus*, which had a long neck and probably a small head like *Plesiosaurus*, but with a very different type of pectoral girdle. Thus the coracoids had no median production in advance of the glenoid cavity; while the scapulæ were large, and articulated together in the median line, and posteriorly were united by their whole length with the coracoids, leaving only very minute coracoidal foramina. If an interclavicle were present it had become fused with the scapulæ. The type species is from the Lower Lias, but there is another in the Upper Lias. The largest genus of the family is, however, *Cimoliosaurus*, in which we may conveniently include those forms described under the names of *Discosaurus*, *Elasmosaurus*, *Mauisaurus*, *Polycotylus*, *Muræosaurus*, and *Colymbosaurus*. This genus was originally described upon the evidence of a very large species from the Cretaceous of New Jersey, with which *Discosaurus*, and probably *Elasmosaurus*, are specifically identical. The New Zealand Cretaceous species described as *Mauisaurus* is closely allied; and it has yet to be proved that the type species is even specifically distinct from the European *C. constrictus*. Many of the other species differ considerably from these typical forms, but if generic divisions are once made it seems impossible to know when to stop.

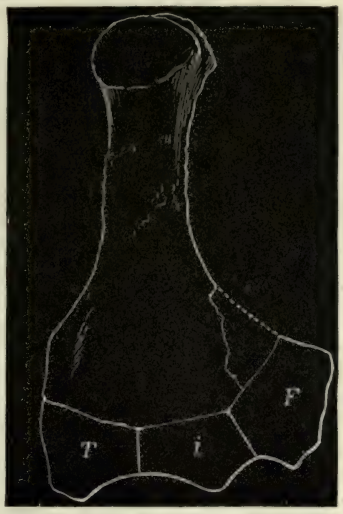


Fig. 998. — Ventral aspect of the right humerus, radius (*T*), ulna (*i*), and pisiform (*F*) of *Cimoliosaurus trochanterius*; from the Kimeridge Clay of Dorsetshire. Reduced. (After Hulke.)

The genus in the above extended series may be characterised as follows. The teeth and skull are relatively small, the mandibular symphysis is short, and the neck usually very long, with the anterior vertebræ relatively small. The vertebræ are more or less elongated, and generally have the neural arches and the cervical ribs completely anchylosed to the centra in the adult; the costal articulations always forming single facets in the cervical region. In the pectoral girdle (fig. 988) the scapulæ have very large and wide ventral plates, meeting in the middle line, without any trace of an interclavicle, and usually sending down a median process to join the coracoids, and thus com-

pletely closing the scapulo-coracoidal foramen.[1] The humerus (fig. 998) is usually longer than the femur; and both these elements may articulate distally with either two or three (figs. 998, 999, 1000) bones, which in the later instances lose all resemblance to the normal elongated form. The ischia are relatively short.

This genus may be divided into two groups, according to whether the vertebral centra have nearly flat or deeply cupped centra. In the former group we have the large *C. truncatus* of the Kimeridge, and the smaller *C. plicatus* (fig. 1000 *bis*) and *C. Richardsoni* (fig. 1000) of the Oxford Clay, in both of which the humerus articulates only with the radius and ulna; the latter species being distinguished by its shorter cervical vertebræ.

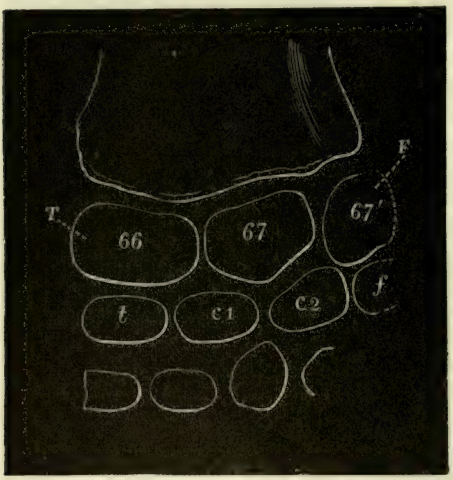


Fig. 999.—Ventral aspect of part of the right pelvic limb of *Cimoliosaurus portlandicus*; from the Portland Oolite. Reduced. *T*, Preaxial; *F*, Postaxial border; 66, Tibia; 67, Fibula; 67′, Homologue of the pisiform; *t*, Tibiale; *c* 1, Intermedium; *c* 2, Fibulare; *f*, Postaxial tarsal. (After Hulke.)

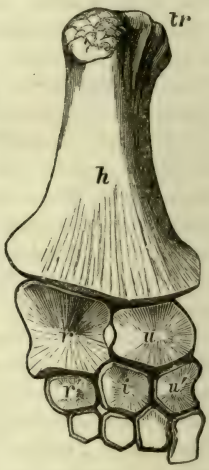


Fig. 1000. — Ventral aspect of part of the right pectoral limb of *Cimoliosaurus Richardsoni*; from the Oxford Clay. One-eighth natural size. *h*, Humerus; *tr*, Trochanter of do.; *r*, Radius; *u*, Ulna; *r'*, Radiale; *i*, Intermedium; *u'*, Ulnare. (After Mansel-Pleydell.)

In *C. portlandicus*, of the Portland Oolite and Purbeck, there were three short bones articulating with the humerus and femur (fig. 999). It is in the Cretaceous, however, that we meet with the largest representatives of this group, which comprise *C. constrictus*, of the European Gault and Chalk; *C. vetustus* and *C. platyurus*, of the Cretaceous of North America; and *C. Haasti*, in the corresponding strata of New Zealand. These were enormous reptiles, with an estimated length of between 30

[1] Occasionally, as in *C. durobrivensis*, of the Oxford Clay, this bar may be absent, but it is not known whether this is only an individual peculiarity.

and 40 feet, and having nearly 40 cervical vertebræ. In the second group, which apparently corresponds to the genus *Polycotylus* of Professor Cope, we have, in the Oxford Clay, *C. oxoniensis* and *C. eurymerus*, in which the humerus articulates with only the radius and ulna, and in

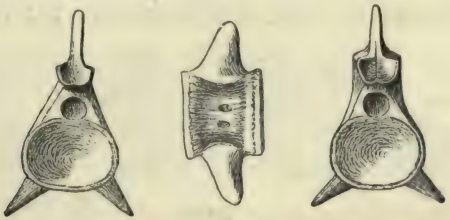


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Fig. 1000 *bis.*—A cervical vertebra of *Cimoliosaurus plicatus;* from the Oxford Clay. One-fifth natural size. 1, Posterior; 2, Inferior; 3, Anterior aspect. (After Phillips.)

the Kimeridge the larger *C. trochanterius*, in which the pisiform also joins the humerus (fig. 998). The very small *C. valdensis*, of the Wealden, may have been of freshwater habits; while in the Chalk we find the larger *C. Bernhardi*. This group appears to have been also represented in the Cretaceous of North America and New Zealand. A species from the Cretaceous of Kansas, described under the name of *Trinacromeron*, has three bones articulating with the humerus.

Fig. 1001.—Dorsal aspect of part of the left pelvic limb of *Peloneustes philarchus;* from the Oxford Clay. One-sixth natural size. *fe*, Distal half of femur; *t*, Tibia; *f*, Fibula; *t'*, Tibiale; *i*, Intermedium; *f'*, Fibulare. The tibia is drawn rather too small in proportion to the fibula.

The imperfectly known genus *Polyptychodon* (*Lutkesaurus*), of the Middle and Upper Cretaceous of Europe, appears to be allied to *Cimoliosaurus*, but with a relatively larger head and teeth, and probably with a much shorter neck. The teeth, which are very abundant in the Cambridge Greensand, have subconical crowns, with strongly-marked ridges, of which a considerable number generally stop short of the summit. These Reptiles must have attained huge dimensions. The genera we have now to consider indicate a different branch from that to which the two preceding genera belong. The first of these is *Thaumatosaurus* (in which *Rhomaleosaurus* may be included), typically occurring in the Great Oolite of Würtemberg, but extending downwards to the Lower Lias and upwards to the Kimeridge Clay of England. In these forms the skull and teeth were relatively large, the latter being often carinated, and the mandibular symphysis (fig. 996, B) comparatively short, with the first five or six teeth enlarged. The neck

was short, and the cervical vertebræ have comparatively short and distinctly cupped subcylindrical centra, carrying double costal facets; while the arches and cervical ribs were firmly articulated to the centra. In the pectoral girdle the scapulæ and coracoids were of the general type of those of *Plesiosaurus;* but the clavicular

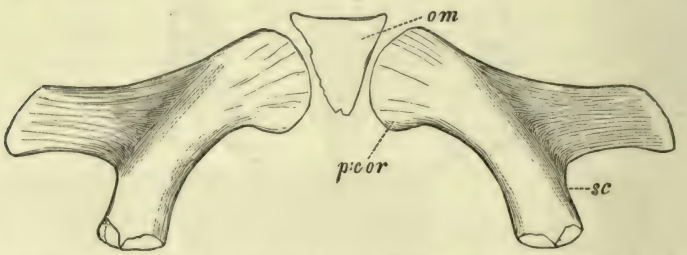

Fig. 1002.—Anterior part of the pectoral girdle of *Peloneustes philarchus;* from the Oxford Clay. Reduced. *om*, Interclavicle; *sc*, Scapula; *p.cor*, Ventral plate of do. The ventral aspect is shown.

arch was greatly elongated transversely, and was probably overlapped by the scapulæ. The humerus was longer or shorter than the femur, and articulated only with the radius and ulna, which were considerably elongated, and separated by a distinct interval. This genus is represented in the Lower Lias by *T. megacephalus* and *T. arcuatus*, and in the Upper Lias by the gigantic *T. Cramptoni*, which attained a length of some twenty feet. The type species, only known by detached teeth and vertebræ, occurs in the Great Oolite of the Continent; while *T. indicus* (fig. 996, B) is found in the Upper Jurassic of India.

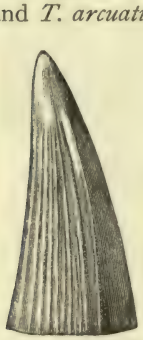

Fig. 1003.—Crown of a tooth of *Pliosaurus brachydirus;* from the Kimeridge Clay of Ely. One-half natural size.

In the genus *Peloneustes*, of the Oxford and Kimeridge Clays, the coracoids (fig. 1001) do not appear to have been produced anteriorly in the middle line; while the scapulæ have their ventral surface broad and flat, and the dorsal surface reduced (fig. 1002). The same figure also shows the extremely small size of the interclavicle. The ischia were very long. The mandibular symphysis (fig. 996, C) is greatly elongated; but the vertebræ agree with those of *Thaumatosaurus* in the firm attachment of the arches and cervical ribs to the centra, although the centra themselves have the terminal faces flatter, and with a transversely elliptical and somewhat angulated contour. The radius and ulna are nearly as broad as long, and have only a very small interval between them. The most specialised genus of this branch is *Pliosaurus* (*Ischyrodon*, *Spondylosaurus* or *Lio-*

pleurodon), which thus occupies a somewhat similar position to the one held by *Polyptychodon* in the preceding branch. This genus is represented by several species of gigantic Reptiles ranging from the Oxford to the Kimeridge Clay, but of which derived remains are also found in the Lower Greensand of Potton, in Bedfordshire. The skull and teeth (fig. 1003) are relatively very large; the former having a somewhat shorter mandibular symphysis than in *Peloneustes*. The teeth are carinated, and in the Kimeridgian species the space between the two carinæ is nearly flat, and

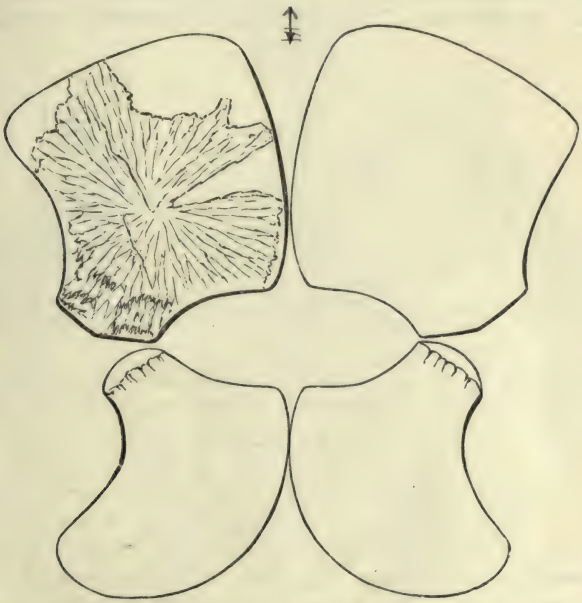

Fig. 1004.—Diagram of the ventral aspect of the pelvic girdle of a young Pliosaur. The upper bones are the pubes, and the lower the ischia. In the adult the ischia become more elongated, and their inner borders should have been placed more nearly parallel. (After Phillips.)

devoid of ridges. The neck is very short, and all the cervical vertebræ (fig. 1005) are relatively large, with nearly flat terminal faces to the very short centra, which in the anterior region have two distinct and often very prominent costal facets. A peculiar feature of all the vertebræ is, that the arches were only articulated to the centra by cartilage, so that they are always found detached. The pectoral girdle was of the general type of that of *Peloneustes*, but it is not improbable that the interclavicle was absent. The humerus was shorter than the femur, and the adius and ulna in the Kimeridgian forms have become much

shorter than in that genus, and have scarcely any intervening space, but in one of the species from the Oxford Clay they have the same form as in the latter. The general arrangement of the ventral bones of the pelvis is shown in the woodcut. In the huge *P. macromerus*, of the Kimeridge Clay, the length of the lower jaw was nearly six feet, and that of the femur one yard, by which some estimate can be formed of the gigantic dimensions attained by the entire animal. Pliosaurs were widely distributed over Europe, and have been described from England, Germany (as *Ischyrodon*), France (as *Liopleurodon*), and Russia (as *Spondylosaurus*). No remains of this genus have, however, been hitherto

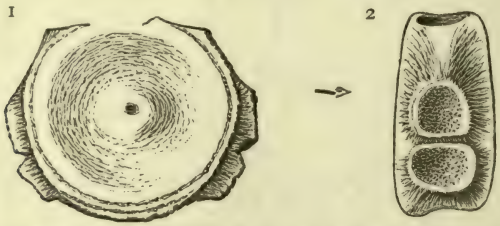

Fig. 1005.—Anterior (1) and lateral (2) aspects of an anterior cervical vertebra of *Pliosaurus macromerus*; from the Kimeridge Clay. One-fifth natural size. (After Phillips.)

recorded from America. The less specialised characters of the Oxfordian forms, as shown by the structure of the teeth, and the longer radius and ulna, indicate affinity with *Peloneustes*.

Finally, it may be mentioned that in addition to the names already recorded the terms *Piptomerus*, *Orophosaurus*, and *Uronautes* have been applied by Professor Cope to Sauropterygian remains from the Cretaceous of North America; while a tooth from the Kimeridgian of France, described under the name of *Hæmatosaurus*, has likewise been shown to belong to this order, although originally regarded as Crocodilian.

Order III. Chelonia.—With the Tortoises, Turtles, and their allies, we enter upon the consideration of the first of the existing orders of Reptiles. In this order the cervical and dorsal vertebræ are not numerous; the body is short and wide, and has a more or less complete bony shell, of which the ventral part, or plastron, consists of few elements of dermal origin, while the dorsal, or carapace, may be in great part of endoskeletal origin. There is generally a horny epidermal exoskeleton. The skull may occasionally have two temporal arcades, but more generally only the lower one is present (fig. 1007), and in some cases even that may be absent. The nares (fig. 1024) are single and terminal; the premaxillæ very small; and there is no parietal foramen in the adult; but there is a distinct

opisthotic bone (fig. 1024). The dentary bones of the mandible are generally fused together; the postorbital is welded with the postfrontal, and usually the prefrontal with the nasal; while the supraoccipital is prolonged backwards. There is no transverse bone. The palate is completely closed by the junction of the pterygoids with the basisphenoid, and often with one another (fig. 1017 *bis*). In all existing forms teeth are absent, and the trenchant jaws ensheathed in horn. Each rib articulates at the junction of two vertebræ; there are

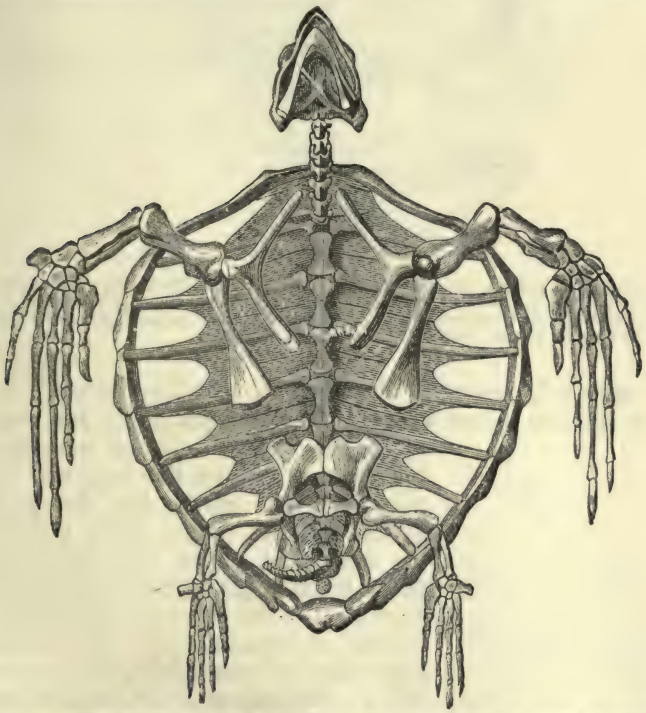

Fig. 1006.—Ventral aspect of the skeleton of a young Loggerhead Turtle (*Thalassochelys caretta*), with the plastron removed. Much reduced. The coracoid and precoracoid of opposite sides are here represented as widely separated from one another. (After Owen.)

no ribs in the cervical region, and no transverse processes to the dorsal vertebræ. The vertebræ may have procœlous, opisthocœlous, or amphicœlous centra in different parts of the column of the same individual. In the pectoral girdle (fig. 1008), which is situated within the ribs, the coracoid is the widest of the three cartilage bones; and the coracoid and precoracoid of opposite sides are respectively connected in the middle line by ligamentous tissue only. The connection between the scapula and precoracoid is short, and there is

no trace of a sternum. In the plastron (fig. 1009), developed on the ventral aspect, the *epiplastrals* (*es*) and *entoplastral* (*s*) correspond to the three plates of the Labyrinthodont thoracic buckler,

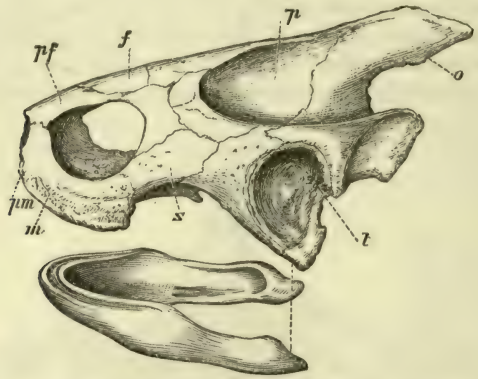

Fig. 1007.—Left lateral aspect of the skull of *Testudo*. *pm*, Premaxilla; *m*, Maxilla; *pf*, Prefrontal and nasal; *f*, Frontal; *p*, Parietal; *o*, Supraoccipital; *z*, Jugal, behind which is the quadratojugal, and above the postfrontal; *t*, Quadrate, showing the incompleteness of the tympanic ring posteriorly; the bone above this ring is the squamosal.

and apparently represent the clavicles and interclavicle. There are in addition paired *hyo-*, *hypo-*, and *xiphiplastrals;* and in some forms (fig. 1012) there are *mesoplastrals* intercalated between the hyo- and hypoplastrals. The pelvic, like the pectoral girdle, becomes in the adult placed on the inner side of the ribs, and has the pubis much larger than the ischium (fig. 1006). The two latter may be anchylosed to the xiphiplastral, and the obturator notch may be converted into a foramen. The humerus has an ectepicondylar groove, which is occasionally converted into a foramen. There is a centrale in the carpus (fig. 829), and in the *Chelydridæ* also in the tarsus. The tarsus may probably be regarded as having five distinct tarsalia, as in the Amphibia and *Mesosaurus*. In both the manus and pes there are always five digits, with a variable number of phalangeals. Not unfrequently the bones of the palate develop inferior plates to floor the nasal passage, and thus produce secondary posterior nares with a vertical aperture. Since the palæonto-

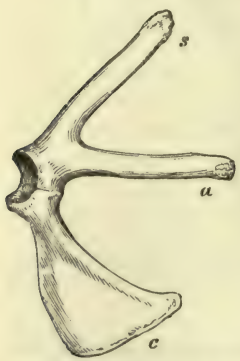

Fig. 1008.—Right side of the pectoral girdle of *Testudo*. *s*, Scapula; *a*, Precoracoid; *c*, Coracoid.

logist generally has to deal with what is frequently and conveniently termed the *shell*,—that is, the carapace and plastron together,—attention must be more particularly directed to its structure in the more typical forms. Commencing with the epidermal skeleton of those forms in which this is fully developed, we find that it consists of horny shields, which usually have their edges in apposition, but occasionally overlap (fig. 1021). On the upper surface there are five *vertebral* shields in the middle line, on either side of which there are four *costals;* while the border has 24 or 25 smaller shields, of which the median anterior one (when present) is termed the *nuchal*, and the double or single posterior shields are known

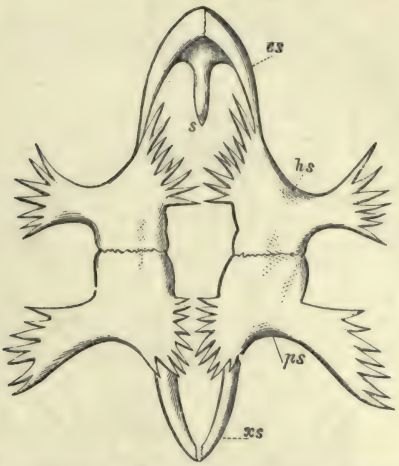

Fig. 1009.—Bones of the plastron of *Thalassochelys caretta*. Much reduced. *es*, Epiplastral (clavicle); *s*, Entoplastral (interclavicle); *hs*, Hyoplastral; *ps*, Hypoplastral; *xs*, Xiphiplastral. (After Owen.)

as the *caudals;* the remaining eleven on either side being reckoned as *marginals*. The position of all these shields is exhibited in fig. 1017. On the ventral aspect of the plastron (fig. 1016) there are usually six pairs of shields, of which the most anterior are termed *gulars*, the next *humerals* (*postgulars*); the next *pectorals;* then the *abdominals;* the *femorals;* and finally the *anals*. In some cases, however, there is an additional *intergular* (very rarely double), which is usually (as in fig. 1012) placed between the gulars, but in some cases may be situated below the gulars, being then surrounded by the gulars, humerals, and pectorals, as in *Chelodina*. In the extinct *Archæochelys*, of the Wealden, where the intergular occupies the latter position, there is also a series of apparently single *interpectoral*, *interabdominal*, and *inter-*

femoral shields dividing the normal pairs of plastral shields; and it is probable that this may be regarded as the archaic type. Similarly in a Chelonian, mentioned below under the name of *Tropidemys*, there is a median series of intervertebral shields dividing the normal vertebrals into two lateral rows. In some cases *inframarginal* shields separate the marginal from the plastral shields.

The bones of the carapace, although following the same general arrangement, do not, as will be seen from the figures, by any means

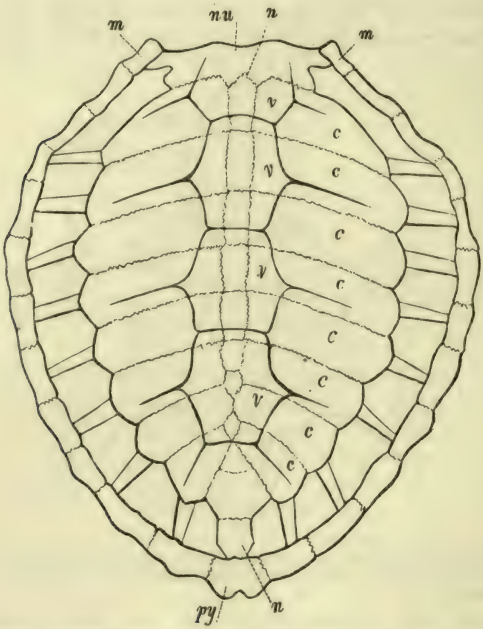

Fig. 1009 *bis*.—Upper surface of the carapace of *Thalassochelys caretta*, with the epidermal shields removed. The dark lines in the middle region indicate the boundaries of the shields, and the sinuous ones the sutures between the bones. *nu*, Nuchal bone; *py*, Pygal do.; the bone above this marked *n* and the next are the suprapygals; above these, the eight neurals, of which the first is marked *n*; *c*, *c*, Costal bones; *m*, *m*, Marginal do.; *v*, *v*, Vertebral shields. Much reduced. (After Owen.)

correspond with the overlying shields. In those forms with a well-developed carapace there are typically (fig. 1017) eight median *neural* bones formed by the expansion of the spines of the dorsal vertebræ (fig. 1010); these being preceded by a *nuchal*, and followed by two or more *suprapygals* and a *pygal*, all of which have no connection with the vertebræ. While, however, the nuchal is a cartilage bone, the pygal and suprapygals are of purely dermal origin. On either side of this median row is a series of from seven to nine

costal bones (fig. 1009 *bis*) formed by the development of a plate on the outer surface of each rib (fig. 1010); while the sides of the carapace are completed by the eleven *marginals*,[1] which are dermal ossifications, and eight of which receive the extremities of the ribs from the second to the ninth. In all young individuals, and in many of the marine Turtles (fig. 1009 *bis*), the costal bones do not extend to the extremities of the ribs, and consequently leave vacuities on the inner side of the marginals, but in the land Tortoises and their allies (fig. 1017) the carapace is entirely bony. In some instances, again, the number of neural bones may be reduced (as in fig. 1014, where there are but seven), and very rarely they are entirely wanting, so that all the costals meet in the middle line. The two suprapygals may also be reduced to one, as in fig. 1014. Similar variations occur in respect to the degree of ossification of the plastron; since

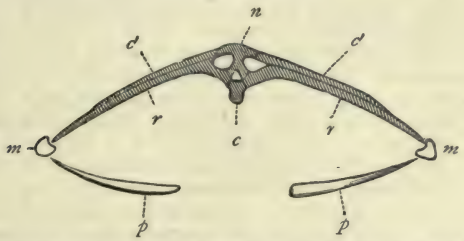

Fig. 1010.—Transverse section through the shell of *Chelone mydas*. Reduced. *c*, Vertebral centrum; *n*, Expanded neural spine; *r*, Rib; *c'*, Costal bone; *m*, Marginal do.; *p*, Plastron. (After Huxley.)

while in all young individuals, and in the existing marine forms (fig. 1009) throughout a great part or the whole of life there are vacuities between the bones, in the land Tortoises and their allies the bones are all connected by suture.

In the marine Turtles the plastron is totally unconnected with the carapace; but in most other forms the hyo- and hypoplastrals send up longer or shorter peduncles underlying the marginals, and in some cases also the costals of the carapace, and thus form well-marked *axillary* and *inguinal buttresses*. These peduncles are longest in some of the existing Pleurodira; while the inward prominence of the buttresses is most marked in the Indian Batagurs.

Considerable variation occurs in the skulls of the different groups, but it can only be mentioned here that in some genera like *Chelydra* and *Chelone* the supratemporal fossa is more or less completely roofed over by the development of plates extending outwards from the parietal and backwards from the postfrontal; this roof being

[1] Occasionally the number of marginals may be increased to twelve or reduced to ten.

most complete among existing forms in *Chelone* and *Dermochelys*, where the parietal joins the squamosal. In such cases, in addition to the inferior temporal arcade formed by the quadrate, quadratojugal, and jugal, as in fig. 1007, there is also a superior arcade constituted by the squamosal and postfrontal. Whereas, however, such arcades in the Crocodilia (fig. 1089) are separated by the infratemporal fossa, in the Chelonia they are in immediate contact.

The feet may either have all the digits free, or enclosed in a common integument to form paddles.

The humerus of existing Chelonians is a very peculiar bone characterised by its extremely prominent globular head; but in certain Jurassic forms (*e.g.*, *Acichelyidæ*) this head was much smaller, so that the bone departs less from a normal type. On either side of this head there is a projecting ridge, of which the radial, or preaxial, one (generally termed the lateral process) corresponds with the deltoid crest of the Crocodilian humerus; while the ulnar or postaxial (mesial) process represents the inner tuberosity of the same. In all Pleurodiran Testudinata the radial process is comparatively small, and the ulnar process placed in the same transverse line as the distal surface of the bone. In many Cryptodira, however, and more especially in the land Tortoises, the radial process forms a thin plate extending towards the ventral aspect, and the ulnar process becomes twisted round to the same aspect; thus causing the pit between the two processes to form a narrow funnel-shaped channel instead of being very broad and open. At the same time the shaft becomes extremely curved. In the marine Turtles, where the shaft is nearly straight, the radial process tends to become aborted, and to attain a position more or less below the head. In the Athecata, which likewise have a nearly straight humerus, the radial process, while descending on the shaft, tends to an excessive development.

In time this order dates from the Upper Trias; and it had attained great development in the Upper Jurassic, from which date it appears to have gone on increasing till the later Tertiary.

Considerable diversity of views obtains as to the classification of the Chelonia, but according to the system now followed in the British Museum it may be divided into the two suborders Athecata and Testudinata.

Suborder 1. Athecata.—This group contains those forms which have been usually regarded as showing the nearest approximation to other Reptiles, and therefore representing the most generalised type of the order. Dr Baur, however, takes the opposite view, and regards them as the most specialised group, which has tended to more or less completely lose the carapace. Before, however, a decisive opinion can be given on this question it must be determined whether the absence of a bony connection in this group between the parietals and pterygoids is to be regarded as an acquired or as an original feature. It may be observed that Dr Baur regards the group as closely allied to the *Chelonidæ*, but if the undermentioned Triassic

genus *Psephoderma* be rightly referred to it, we have at once a great obstacle to the acceptance of his view.

The suborder may be briefly characterised by the circumstance that the carapace is entirely of dermal origin, and quite separate from the vertebræ and ribs, and may consist merely of a series of marginal bones, or of marginals with a single median dorsal row of broad scutes, or of a number of small irregular scutes, with longitudinal rows of larger ones; while the plastron (fig. 1011) has no entoplastral (interclavicular) element. The cranium is characterised by the absence of vertical plates connecting the parietals with the pterygoids. All the forms are of marine habits, and consequently the extremities of the limbs are modified into paddles like those of the *Chelonidæ*.

Before noticing the two established families, it may be observed that the imperfectly known *Psephoderma* of the Upper Trias of Bavaria and England is founded on a specimen which appears to be a carapace of a member of this suborder, although it has been suggested that it is not Chelonian at all. This presumed carapace is formed of a number of polygonal scutes, traversed by longitudinal rows of keeled scutes. Here also may be mentioned the genus *Macellognathus*, founded upon the anterior portion of a toothed mandible from the Upper Jurassic of North America, which Professor Marsh regards as showing affinity with the Chelonia, and which may possibly indicate a generalised family of the present suborder.

Family Protostegidæ.—This family is usually regarded as the least specialised of the two that are yet established, although an opposite view is taken by Dr Baur. The carapace, according to the interpretation of that authority, is represented merely by a row of marginal scutes; but the plastron is strongly developed, and composed of very thick ossifications. The type genus *Protostega* occurs typically in the Cretaceous of North America. It was considered by its describer Professor Cope to have possessed a solid carapace, but the bones which he regarded as probably dorsal appear to belong to the plastron. It was also suggested that the dorsal vertebræ were procœlous, with traces of transverse processes; but these vertebræ are probably referable to the cervical region. The type species attained very large dimensions. An allied form from the Upper Cretaceous of Italy has been described under the name of *Protosphargis* (fig. 1011), but further evidence is required to prove its right to generic distinction from the American form. It has, indeed, been asserted that there were no marginal bones, but according to Dr Baur this is incorrect. In the Cambridge Greensand and the English Chalk there occur humeri of Athecate Chelonians which have been provisionally referred to *Protostega*.

It is uncertain whether the remains from the American Cretaceous described as *Atlantochelys* belong to the last-named genus.

Family Dermochelyidæ.—This family is characterised by having a carapace composed either of a median row of large and broad scutes and lateral marginal rows, or of a mosaic of small irregular scutes, or tessaræ, traversed by longitudinal rows of larger ones. The plastron varies considerably; and the humerus, which is of the flattened type of that of the *Chelonidæ*, is distinguished from that of the preceding family by the great development of its radial pro-

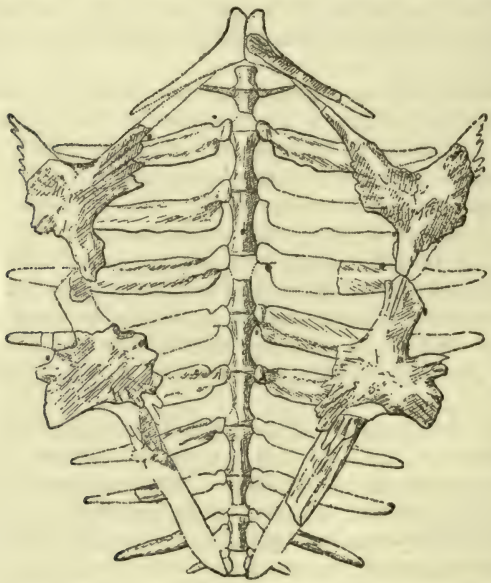

Fig. 1011.—Ventral aspect of the plastron and thoracic region of *Protosphargis veronensis*; from the Upper Cretaceous of Italy. One-fifteenth natural size. (After Capellini.)

cess, which is situated near the middle of the shaft. The skull has the temporal fossæ completely roofed, as in the *Chelonidæ*, and an open tympanic ring, but has no bony floor beneath the narial passage. Whereas all the members of the preceding family are of moderate size, several representatives of the present one attained huge dimensions. The earliest representative is the genus *Eosphargis*, of the London Clay, of which the one known species was originally described as *Chelone gigas*. The skull is of the general type of that of the next genus, but the carapace apparently consists only of a median row of very broad and large carinated scutes, and also of a row of marginals; the structure of the plastron is not definitely

known, but it was doubtless devoid of tessaræ. The allied *Psephophorus*, ranging in Europe from the Middle Eocene to the Upper Miocene, and also found in the Upper Eocene of the United States, is characterised by the presence of a complete tesselated carapace and plastron. In the carapace the longitudinal rows of larger scutes are not carinated, and are more approximated than in the existing genus; the carapace is also thicker than in the latter; and there are larger marginals. It is also suggested that the carapace may have had horny epidermal shields. The skull is short and much depressed. The existing genus *Dermochelys* (*Sphargis*) is represented only by the well-known Leathery-turtle, and is characterised by the absence of a tesselated plastron; by the carination of the scutes of the larger rows of the carapace; by the comparative thinness of the carapace, which is devoid of epidermal shields; and by the longer and more vaulted skull. It is, moreover, worthy of note that in this, as in the preceding genus, there is a distinct nuchal bone at the anterior extremity of the carapace, corresponding to the nuchal of the Testudinata; but there are no marginal ossifications. The one existing species of *Dermochelys* attains a length of nearly five feet, but a species of *Psephophorus* is estimated to have been as much as ten feet in length. The skull of *Eosphargis*, although much larger than that of *Psephophorus*, does not apparently indicate a much larger carapace.

Suborder 2. Testudinata.—This suborder, for which the name Thecophora[1] is also employed, includes by far the great majority of the order, or all those forms commonly known as Tortoises, Terrapins, and Turtles. The group is characterised by the middle region of the carapace being formed of bony plates, developed primarily from the ribs and the neural spines of the dorsal vertebræ, to which it is firmly welded. The outer surface of the carapace is very generally smooth and overlain by horny epidermal shields, but it may be sculptured and devoid of such shields. The parietal bones of the skull in all cases send down vertical descending plates, which may either unite directly with the pterygoids, or be separated therefrom by the intervention of the columella or epipterygoid. It may be observed that in nearly all the Mesozoic forms the vertebral shields are very wide, and that this condition obtains in the young of the later forms. This suborder may be divided into four sections; one, and not improbably two, families of the third section being of marine habits.

Section 1. Amphichelydia.—This section is formed for the reception of certain extinct Chelonians, mostly of Mesozoic age, which combine in a remarkable manner the characters of the two fol-

[1] This name is objectionable, as being employed for an order of Hydroid Zoophytes (*vide supra*, vol. i. p. 203).

lowing sections, and may probably be regarded as the survivors of the earlier ancestral types from which those two sections took origin. They are all characterised by the presence of a mesoplastral bone, and of an intergular shield in the plastron; and the pelvis may or may not be connected with the xiphiplastrals. The entoplastral is rhomboidal. The skull and cervical vertebræ are unknown.

Family Pleurosternidæ.—All the members of this section may be, at least provisionally, included in this family. In addition to the characters given above, it may be observed that the shell is fully ossified, and that the carapace has a complete series of neural bones, of which the hindmost articulates with the anterior suprapygal bone. On the supposition that the Chelonian plastron is derived from a system of abdominal ribs like those of the Rhynchocephalia and Sauropterygia, it will be evident that the mesoplastral of the present group is an archaic feature.

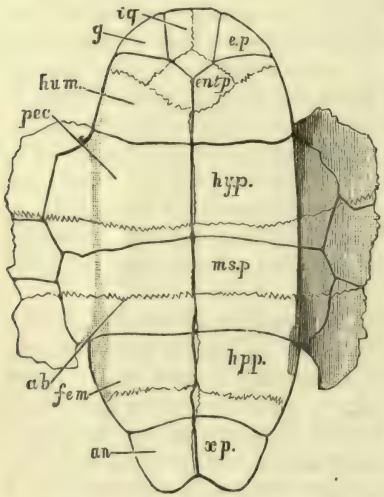

Fig. 1012.—The plastron of *Pleurosternum Bullocki*; from the Purbeck of Dorsetshire. One-third natural size. *ig*, Intergular scute; *g*, Gular do.; *pec*, Pectoral do.; *ab*, Abdominal do.; *fem*, Femoral do.; *an*, Anal do.; *e.p*, Epiplastral bone; *entp*, Entoplastral do.; *hy.p*, Hyoplastral do.; *ms.p*, Mesoplastral do.; *hp.p*, Hypoplastral do.; *xp*, Xiphiplastral do.

In the typical genus *Pleurosternum* (*Megasternum* or *Digerrhum*), which occurs commonly in the English Purbeck, and is also found in the Portland Oolite, the shell is broad and depressed, with complete mesoplastrals (fig. 1012), a large and wide entoplastral, a single intergular shield, and no nuchal shield. In the adult the pubis articulates with a smooth facet on the xiphiplastral, thus foreshadowing the complete sutural union which occurs between these bones in the Pleurodira; but in the young it appears that there was no such articulation. The neural bones of the carapace are hexagonal and comparatively long; while the vertebral shields (as in so many of the earlier Chelonians) were relatively wide. Further, inframarginal shields (shown in fig. 1012) were developed between the shields of the plastron and the marginal shields of the carapace; while the extremities of the xiphiplastrals were notched. The bones of the pectoral girdle and the humerus approximate to those of the existing Pleurodiran genus *Chelys*.

Much confusion has arisen in regard to this genus owing to a plastron having been described under the name of *Platemys Bullocki*, under the erroneous impression that it had been obtained from the London Clay. Remains of *Pleurosternum* are extraordinarily abundant in the Purbeck of Dorsetshire; and include specimens of all ages, from the newly hatched young, with a carapace of a couple of inches in length, to adult specimens which are close upon twenty inches. Curiously enough, however, no specimen of the skull seems to have been obtained. The young appears to have differed considerably in the details of the shell from the adult; thus, not only was the pubis, as already mentioned, entirely unconnected with the plastron, but the marginal bones encroached in a remarkable manner upon the front of the nuchal. Moreover, it seems that in very young individuals the vertebral shields were divided in the middle.

In *Helochelys*, of the Lower Greensand of Bavaria, we have another genus also furnished with complete mesoplastrals, but apparently without any articulation between the pubis and the plastron. The shell is ornamented with a pustular sculpture resembling that found in the genus *Tretosternum*, mentioned below among the *Chelydridæ*. The plastron differs from that of *Pleurosternum* in that the xiphiplastrals were not notched; and there appears to have been a nuchal shield.

The next two genera, constituting the family *Baënidæ* of Professor Cope, may be at least provisionally placed here. Both are devoid of a bony attachment between the pelvis and plastron. The genus *Platychelys* (*Helemys*), typically from the Lower Kimeridgian lithographic limestone of the Continent, is readily distinguished by the number of irregular ridges and prominences on the carapace (fig. 1013), and by the width and irregular contour of the neural bones. The mesoplastrals are small, and widely separated in the middle line; and the intergular shield is single.

The genus *Baëna*, from the Eocene of the United States, has the mesoplastrals meeting only by a point in the middle; and is further remarkable for the presence of double intergular shields, and the presence of a small additional costal shield in advance of the normal first costal. The caudal vertebræ are opisthocœlous. Professor Cope, who places this genus in the Cryptodira, regards it as indicating a generalised type, showing marked signs of affinity with the Pleurodira, and exhibiting traces of an imperfect connection between the pelvis and the plastron. The extinct North American genus *Polythorax* should perhaps be also placed in this family, although it is not certain that it is not allied to the Cryptodiran *Adocus*.

Here also may be mentioned the very imperfectly known genus *Archæochelys*, of the English Wealden, in which, as observed above,

the paired shields of the plastron were separated by a median series of azygous shields, which probably extended backwards from the intergular to the extremity of the xiphiplastral. If the separate bones are rightly interpreted, it would appear that the plastron had a mesoplastral element, which, instead of being situated in the middle of the bony bridge as in *Pleurosternum* (fig. 1012), and taking no part in the formation of the axillary notch, formed the anterior part of this bridge and the whole of the notch. The hyoplastral would therefore be entirely above the latter notch, as in the existing Pleu-

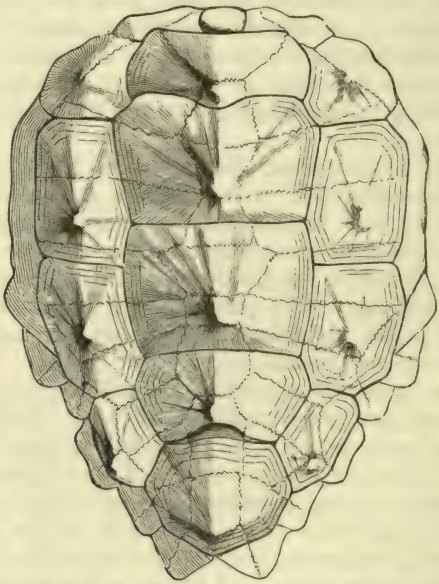

Fig. 1013.—Carapace of *Platychelys Oberndorferi*; from the Lower Kimeridgian of Bavaria. One-third natural size. (After Wagner.)

rodiran genus *Sternothœrus*. Possibly also a Chelonian, from the Lower Jurassic of Stonesfield, described, upon the evidence of the impressions of the epidermal shields of the carapace, under the name of *Testudo Stricklandi*, should also find a place in this group. The name *Protochelys* may be proposed for this form, which has certainly nothing to do with *Testudo*.

Section 2. Pleurodira.—The members of this section are, as a rule, characterised by the complete ossification and union of the carapace and plastron, and by the full development of the marginal bones, which are connected with the ribs, as well as by the sutural union or anchylosis (synostosis) of the pelvis with both the carapace and the xiphiplastral part of the plastron. Very frequently the first

suprapygal bone, and some (fig. 1014) or occasionally all of the neural bones are absent; and when epidermal shields are developed an intergular (as in fig. 1012) is present on the plastron. This shield is, however, sometimes found in the next section, in which the neurals may also be reduced in number. The entoplastral bone (as in the preceding section) is either oval or rhomboidal; and a mesoplastral bone (compare fig. 1012) may be present.

In the skull of existing and Tertiary types the tympanic cavity is completely surrounded by the quadrate, which forms an unbroken ring; the articular surface of the quadrate has a concavity for the reception of a condyle on the mandible; the pterygoids are very broad and wing-like; the vomer may be absent, so that the palatines may meet in the middle line; and there may be distinct nasals, and a suture in the mandibular symphysis. The cervical vertebræ have well-developed transverse processes, and single terminal articulations; while there are never more than three phalangeals to the digits.

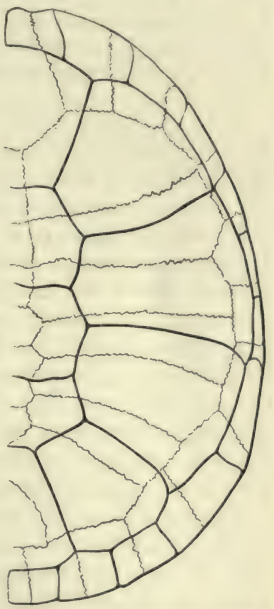

Fig. 1014.—The right half of the carapace of *Sternothærus nigricans*; from Madagascar. The thick lines indicate the boundaries of the epidermal shields.

The Pleurodira are further characterised by their inability to retract the head directly within the carapace; but the neck is bent on one side and the head thus brought within the margin of the shell. In all cases the labyrinth of the ear is completely open from behind.

At the present day this section is almost exclusively confined to the southern hemisphere; but in the Eocene forms more or less nearly allied to existing types were widely spread over the northern hemisphere, and in the Mesozoic there were many European representatives of the group. With the exception of *Podocnemis*, the existing forms are carnivorous, and the whole of them are thoroughly aquatic.

At least one of the two earliest known genera of Testudinata has been referred to this section; and from the occurrence in many existing forms of separate nasals, and of a mesoplastral bone, we may regard this section as retaining evidence of a close alliance with a primitive generalised type which has been lost among existing Cryptodira, since it is nearly certain that features like these if once lost would not reappear, except as abnormalities. The presence of transverse processes to the cervical

vertebræ would also seem to be a generalised character; and, from the evidence afforded by the above-mentioned *Pleurosternum* and *Archæochelys*, the presence of an intergular shield should probably be likewise regarded in the same light. The anchylosis of the pelvis to the plastron, as pointed out by M. Dollo, would, however, seem to prevent us from regarding the Pleurodira as the ancestors of the Cryptodira; and it is more probable that both sections should be regarded as divergent branches of a common stock, probably represented by Amphichelydia of earlier age than those yet known.

It would seem probable that the palate of the earlier Mesozoic Pleurodirans approximated to the Cryptodiran type, and that the peculiar mandibular articulation and closed tympanic ring of the existing forms are acquired features. The skull of the Mesozoic types appears generally to have been roofed over after the fashion of the modern Turtles; this structure having apparently been common to many of the earlier forms of both this and the following sections of the suborder.

Family Proganochelyidæ. — This name is proposed by Dr Baur for the reception of the genus *Proganochelys*, from the Keuper of Würtemberg, which he regards as a Pleurodiran, although differing from all other members of the section in that the plastron unites only with the edges of the marginals, without giving off axillary and inguinal buttresses. It is suggested that mesoplastral bones were present, while the carapace is compared to that of *Platychelys*. The latter resemblance suggests that this form might belong to the Amphichelydia, but a study of the figure of the type specimen given by Professor Quenstedt, under the synonym of *Psammochelys*, shows that its extremely imperfect nature scarcely permits any decisive opinion to be formed as to its true affinities. Whether the imperfectly known and apparently aberrant genus *Chelytherium* of the Keuper is an allied form cannot yet be determined.

Family Plesiochelyidæ.—This Mesozoic family is characterised by the total absence of the mesoplastral element in the plastron, and also by the circumstance that the pubis alone is united with the xiphiplastral; while there may or may not be a complete series of neural bones articulating posteriorly with the suprapygal. The plastral shields are separated from the marginals by the intervention of a series of inframarginals; and the plastron, as in the succeeding families, is connected by long buttresses with the carapace. The humerus is of the type found in existing Pleurodira; and the second digit of the manus, when known, has but two phalangeals. The skull is known only in a few cases with certainty.

The typical genus *Plesiochelys* and the closely allied *Craspedochelys* were originally described from the Lower Kimeridgian Lithographic limestones of Bavaria and France. These genera have a thick shell, with the full complement of neural bones, which posteriorly join the first suprapygal, and with the vertebral shields of the carapace of moderate width. The entoplastral bone is relatively wide and

rounded; the nuchal is but slightly emarginate; and the intergular shield is double. The surface of the carapace is usually marked by flutings. Some at least of the Chelonians from the Kimeridgian of Hanover which have been described under the preoccupied name of *Stylemys* may be included in *Plesiochelys*, and this genus is also represented in the English Wealden.

Allied Chelonians, from the Kimeridgian of Hanover, described under the name of *Chelonides* (likewise preoccupied), not improbably indicate forms connecting *Plesiochelys* with the undermentioned *Hylæochelys*. In one specimen referred to the type species of *Chelonides*, there are but seven neural bones; but the vertebral shields are narrower than in typical species of *Hylæochelys*. If these forms are really entitled to rank as a distinct genus they require a new name. A skull said to have been associated with the shell of the type species of *Chelonides* has the temporal fossæ roofed over by bone, while the palatines are described as meeting in the middle line after the manner of many existing Pleurodira. From the occurrence of *Plesiochelys* and the undermentioned *Hylæochelys* in the Wealden, and the apparent rarity of the *Acichelyidæ* in the same beds, it is probable that the members of this family were of freshwater habits.

It is probable that the genus *Parachelys* of the Lithographic Limestone (which was considered by Professor von Zittel to be indistinguishable from *Acichelys*) is really identical with *Plesiochelys;* in which case the former name should supersede the latter, and the family name *Parachelyidæ* replace *Plesiochelyidæ*. The humerus of this genus resembles that of recent Pleurodira, and is widely different from that type of humerus which appears to be referable to the *Acichelyidæ*. The number of the phalangeals in the digits of the manus of this form (and also in *Idiochelys*) is 2, 2, 3, 3, 3; and this presents a decided approximation to the existing Pleurodiran genus *Pelomedusa*, which differs from all other freshwater forms now living in that there are only two phalangeals in each digit.

The name *Hylæochelys* has been proposed for an allied genus of Chelonians typically represented by the so-called *Pleurosternum latiscutatum* of the English Purbeck, which as shown by a shell from the Wealden preserved in the British Museum, belongs to the present family. This genus is distinguished from *Plesiochelys* by the much wider vertebral shields of the carapace, in which the width may exceed three times the length; and also by the narrower and diamond-shaped entoplastral bone; as well as by the circumstance that the neural bones, at least usually, do not join the suprapygals, and are generally interrupted in the middle of the series; while the hypoplastral bone is relatively shorter. Both in this and the preceding genus there may be a vacuity in the middle of the plastron.

It would appear that the Purbeck form described as *Pleurosternum emarginatum*, as well as the Wealden specimens to which the names *Chelone Belli* (*costata*), and *Platemys Dixoni* and *Mantelli* have been applied, are likewise referable to *Hylæochelys*. It is, moreover, very probable that a Chelonian, from the Upper Greensand of Kent, to which the name *Plastremys* has been given without description, is also referable to this genus.

The genus *Idiochelys* (*Chelonemys*) and the allied *Hydropelta*, of the Lower Kimeridgian of the Continent, would appear to be closely allied to the preceding. *Idiochelys* resembles *Hylæochelys* in its extremely wide vertebral shields, and also in its small and diamond-shaped entoplastral bone, but differs in that the number of neural bones is generally much reduced, so that many of the costals meet in the middle line; while there are also differences in the contour of the lower plastral shields. This genus, which is known only by immature specimens, was indeed regarded by Professor Rütimeyer as essentially Pleurodiran, although there was no absolutely decisive evidence in support of this view. The shell is thinner than in *Plesiochelys;* and the skull has the temporal fossæ roofed over by bone, and apparently had a long sutural union between the postfrontal and parietal.

Mesozoic Chelonians of Uncertain Position.—It will be convenient to notice in this place several Mesozoic Chelonians mostly known to us only by the skull, of which the serial position cannot at present be determined. A large skull from the Portland Oolite, originally described as *Chelone platyceps*, but subsequently made the type of the provisional genus *Stegochelys*, is characterised by the incomplete roofing of the temporal fossæ, and the meeting of the prefrontals in the middle line, while it is stated to have distinct nasals. The palate is unknown. The size of this specimen suggests that it may perhaps be referable to the Cryptodiran genus *Thalassemys* of the Kimeridgian.

In the Wealden of Belgium there occur remains of young Chelonians to which the name *Chitracephalus* has been applied. There is no mesoplastral bone; and the skull is characterised by its elongated form, open temporal fossæ, and the approximation of the orbits to the nares.

In the Upper Cretaceous genus *Rhinochelys* the shell is only known by fragments. The skull (fig. 1014 *bis*) has an inferior temporal arcade, the temporal fossæ are completely roofed over, the palatines meet in the middle line, the nasals are distinct from the prefrontals, which are separated from one another by the frontals, the pterygoids are comparatively narrow, and laterally emarginate, while the symphysial suture of the mandible is obliterated. The humerus is of the Pleurodiran type found in *Para-*

chelys. It has been suggested that this genus is Pleurodiran; and if this prove to be the case it will be interesting as showing an approximation in several cranial features to the Cryptodira. In its complete roof the skull of this genus approximates to the *Chelonidæ*. Remains of *Rhinochelys* are very abundant in the Cambridge Greensand, and they are also met with in the Gault and the Lower Chalk. Fragmentary Chelonian shells from the Cambridge Greensand, to which the name *Trachydermochelys* has been applied, are not improbably referable to this genus. They are characterised by their pustulate external surface; the pustules being much larger than in the Amphichelydian genus *Helochelys* of the Lower Greensand. A somewhat similar, although less marked, pustulation occurs in the existing *Chelodina*.

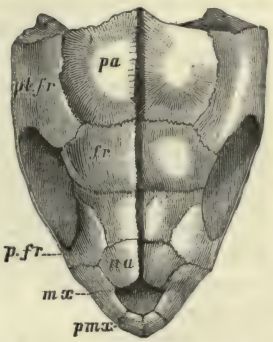

Fig. 1014 *bis*. — The cranium of *Rhinochelys cantabrigiensis*, imperfect posteriorly; from the Cambridge Greensand. *pa*, Parietal; *pt.fr*, Postfrontal; *fr*, Frontal; *p.fr*, Prefrontal; *na*, Nasal; *mx*, Maxilla; *pmx*, Premaxilla.

Family Pelomedusidæ. — Reverting to the consideration of undoubted Pleurodirans the present existing family agrees with the Amphichelydian *Pleurosternidæ* in the presence of mesoplastral bones, but is distinguished in that both the pubis and ischium have a sutural union with the xiphiplastral. The shields of the plastron, as in the next family, are in contact with the marginals, owing to the absence of inframarginals. The skulls of existing types have an infratemporal arcade, and in *Podocnemis*, alone among existing representatives of the section, the temporal fossæ are roofed over; moreover, the prefrontals are in contact in the middle line and are fused with the nasals; the palatines, owing to the absence or abortion of the vomer, meet; and the suture between the dentary bones of the mandible is obliterated. The second cervical vertebra is amphicœlous; and the neck is completely retractile within the shell. Further, the series of neural bones, as in the next family, is incomplete and is not connected with the suprapygals. Finally, in both this and the next family the characters of the tympanic and palatal regions of the skull are those mentioned at the commencement of the description of the Pleurodira. The earliest known representatives of this family occur in the Upper Cretaceous of the United States, where we meet with forms apparently closely allied to the existing *Podocnemis*. The genus *Bothremys* has been described upon the evidence of a skull from those deposits; while the name *Taphrosphys* has been applied to portions of the carapace and

plastron which not improbably belong to the same form. *Bothremys* differs from *Podocnemis* by the presence of a distinct vomer. It is not improbable that allied forms occur in the Cretaceous of New Zealand. The only existing genus which appears to be represented in a fossil state is the above-mentioned *Podocnemis*, of South America and Madagascar, which occurs in the London Clay and the Eocene of Northern India. This genus includes the largest existing representative of the section. The carapace has seven neural bones, and the mesoplastrals are small, and do not meet in the middle line. The shell of a large Chelonian from the London Clay, which has been referred to this genus under the name of *P. Delabechei*, may not improbably belong to the genus *Dacochelys*. The latter is founded on a mandibular symphysis from the same deposits which is characterised by a large spine-like process on its oral surface, and the serrated margins of the alveolar borders. Its serial position depends on whether it is specifically identical with the above-mentioned shell.

Family Chelyidæ.[1]—In this family the shell is much thinner than in *Plesiochelys*, and is characterised by the absence of the mesoplastrals, and the reduced number of neural and suprapygal bones; while both the pubis and ischium unite with the plastron. The skull has an incomplete inferior temporal arcade, owing to the absence of the quadratojugal; and is further distinguished by the separation of the prefrontals by the frontals; the distinct nasals (except in *Chelys*); by the vomer dividing the palatines; and by the persistence of the suture in the mandibular symphysis. The temporal fossæ are open, but there is an arch connecting the parietal with the squamosal, not found in the *Pelomedusidæ*, and which is probably a remnant of the earlier type of roof. The fifth and eighth cervical vertebræ are biconvex. The neck cannot be fully retracted within the carapace. As typical genera we may notice the South American *Chelys*, *Hydraspis*, and *Platemys*; and the Australian *Chelodina*, *Emydura*, and *Elseya*, in which neural bones are absent. Remains of *Chelodina* and *Emydura* occur in the Pleistocene of Australia; while *Hydraspis* is found in a fossil state in the Lower Eocene of India, and *Platemys* has been recorded from the Cretaceous of North America.

Family Miolaniidæ.—This is an extinct family represented only by the remarkable *Miolania*, from the Pleistocene of Australia, of which the remains were originally referred to the large *Varanus* of the same deposits. This family, according to Mr Boulenger, occupies a position in the present section somewhat analogous to that filled by the *Chelydridæ* among the Cryptodira; the caudal vertebræ

[1] Frequently incorrectly given as *Chelydidæ*.

being opisthocœlous and the temporal fossæ of the cranium roofed over by bone. The cranium (fig. 1015) is remarkable for carrying several pairs of horn-like processes (on which account the name *Ceratochelys* has been proposed); and the tail was protected by a nodose bony sheath (fig. 1014), somewhat resembling that of the Glyptodont Edentates. The species of which the skull is shown in the woodcut must have attained huge dimensions. The carapace and plastron are known only by fragments. From the structure of

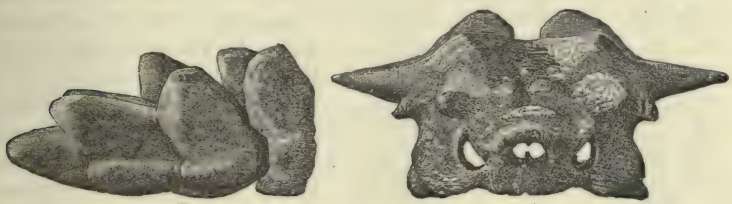

Fig. 1015.—*Miolania Oweni.* A, Anterior view of cranium; B, Right lateral aspect of the extremity of the caudal sheath; from the Pleistocene of Australia. Much reduced. (After Owen.)

the jaws it is inferred that *Miolania* was herbivorous; while the form of the terminal phalangeals and the solid caudal sheath are indicative of terrestrial habits. The bones of the pelvis are fused into an innominate bone, and some of the cervical vertebræ had two transverse processes.

It should be observed that Dr Baur dissents from the view that this genus is a Pleurodiran, and would refer it to the Cryptodiran family *Testudinidæ;* but there appear to be several misconceptions in the arguments adduced in support of this view. Sir R. Owen does not, indeed, recognise the Chelonian nature of *Miolania*, and regards it as constituting a distinct group, under the name of Ceratosauria; but this view is altogether at variance with the facts, and there can be no question but that the genus is a true Chelonian.

Family Carettochelyidæ.—The last family of the Pleurodira is characterised by the absence of horny shields, and is typically represented by *Carettochelys* of New Guinea, in which the neural bones are very small and do not touch one another, and the limbs are paddle-shaped. In the Lower Eocene of Northern India we find the extinct genus *Hemichelys*, which differs from *Carettochelys* in having seven large neural bones in contact with one another; the nature of the limbs being unknown.

Section 3. Cryptodira.—In this section the ossification of the carapace and plastron may be either imperfect or complete, and the two may or may not be connected at their edges; there is no bony attachment of the pelvis to the plastron; and as a general rule, the

full complement of suprapygal and neural bones is present, although there are numerous exceptions. Excluding the Amphichelydian forms, no known Cryptodiran has a mesoplastral bone, while in the majority of cases, especially among existing types, the plastron has no intergular shield (fig. 1016). The entoplastral, when present, is either ovoid, rhomboidal (fig. 1016), or ┼-shaped (fig. 1009), and the epiplastral joins the hyoplastral. In the skull (fig. 1007) the outer border of the tympanic cavity is always deeply notched posteriorly; the quadrate articulates with a concavity in the mandible; and the pterygoids are comparatively narrow and laterally emarginate. There are never more than three phalangeals in the digits. The sacral and caudal ribs (as in the Pleurodira) articulate partly with the centra and partly with the arches of the vertebræ; while the cervical vertebræ have very imperfectly developed transverse processes. No existing Cryptodiran has distinct nasals, and at present there is no decisive evidence of the presence of these bones in any fossil form.

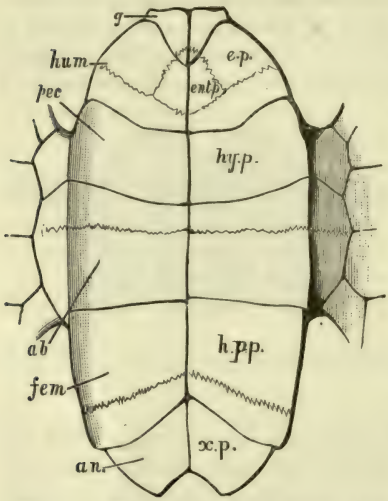

Fig. 1016.—Plastron of *Kachuga tectum*; from India. One-half natural size. *g*, Gular shield; *hum*, Humeral do.; *pec*, Pectoral do.; *ab*, Abdominal do.; *fem*, Femoral do.; *an*, Anal do.; *e.p*, Epiplastral bone; *ent.p*, Entoplastral do.; *hy.p*, Hyoplastral do.; *h.pp*, Hypoplastral do.; *x.p*, Xiphiplastral do.

The Cryptodira are further characterised by their power of retracting the head by a sigmoid curvature of the neck in a vertical plane directly within the carapace. This large section comprises the great majority of the existing Testudinata, and at the present day is mainly characteristic of the Northern Hemisphere, being totally absent from Australia. The habits of existing Cryptodires may be carnivorous or herbivorous, and either terrestrial, fluviatile, or marine.

Family Acichelydæ.—Under this name may be grouped a number of generalised Cryptodirans often spoken of as the *Thalassemydes*, and in some cases as the *Eurysternidæ*. They occur typically in the Lower Kimeridgian Lithographic Limestones of the Continent, and are abundant in the Kimeridge Clay, while they survived till the period of the Lower Greensand. They were probably mainly of marine habits, since they appear to be very rare in the

freshwater Purbeck and Wealden beds. They are characterised by the more or less heart-shaped carapace, of which the costals are often imperfectly ossified, and do not unite completely with the marginals. The plastron has, moreover, a vacuity in the centre, which persists for a long period or throughout life, but it had large axillary and inguinal buttresses for connection with the carapace. The humerus has a very imperfectly developed head and a slightly curved shaft; and the limbs were not modified into paddles. The nuchal bone of the carapace has no costiform processes; and the temporal fossæ of the skull were more or less completely roofed over by bone.

In their cordiform, and frequently imperfectly ossified carapace, the *Acichelyidæ* agree with the modern *Chelonidæ;* and since the peculiar form of the neurals of *Tropidemys* is another feature only met with elsewhere in the latter family, there are strong grounds for regarding the one family as the direct ancestor of the other. This family also exhibits certain signs of affinity with the Pleurodiran *Plesiochelyidæ;* while the simplicity of the humerus is a very generalised character.

The genus *Thalassemys*, which includes some very large forms, is characterised by its long and flat neural bones, in which the anterior lateral surfaces are much shorter than the posterior ones; while the vertebral shields are narrow. The carapace is well ossified, and of considerable thickness. The type species occurs both in the Lithographic Limestone and the Kimeridge Clay of England; the undescribed Chelonian from the latter deposit at Ely, to which the name *Enaliochelys* has been applied, being apparently identical. As already mentioned, the Portlandian *Stegochelys* may likewise be the same; and the genus is represented in the Dorsetshire Purbeck. In the typical genus *Acichelys* (*Eurysternum*,[1] *Achelonia*, *Palæomedusa*, or *Aplax*) the neural bones of the carapace are flat, with short and often indistinct antero-lateral surfaces, and the costals are well ossified, the vertebral shields of the carapace being comparatively wide. This genus seems to be confined to the Lithographic Limestone.

In *Pelobatochelys*, of the Kimeridge Clay, we have a large form with a very imperfectly ossified carapace, in which the costals are extremely thin, and the neural bones are long and six-sided. The antero-lateral surfaces of the neurals are much shorter than the postero-lateral, and in the fifth neural the latter surfaces are deeply excavated. The neurals, especially in the hinder part of the carapace, are strongly ridged, having the form of the ridge-tiles of a roof; and the hinder part of the whole carapace is itself roof-like. The vertebral epidermal shields were very wide, and the borders of

[1] This name is the earliest, but is preoccupied.

the areas which they overlie on the carapace are conspicuously fluted. The last genus, *Tropidemys*, while having the roof-like posterior neurals of *Pelobatochelys*, is distinguished by the almost regularly hexagonal form of these bones, owing to the lengthening of the anterior and the shortening of the posterior lateral surfaces. One species from Hanover referred to this genus shows the unique feature of a median row of numerous small intervertebral shields dividing the normal vertebrals into two lateral series. This genus occurs in the Lithographic Limestone, in the English Kimeridge Clay, and the Lower Greensand of Switzerland (*T. valanginiensis*). The detached neurals are readily distinguished not only by their shape, but by their excessive thickness.

Family Chelydridæ.—This family is confined at the present day to North, and part of South America, where it is represented by the Alligator-terrapins (*Chelydra*), and the larger Snapper (*Macroclemmys*). The skull is more or less triangular, and very broad behind; the temporal fossa is partially roofed over, but the squamosal is widely separated from the parietal; the bones of the palate do not develop plates to floor the narial passage; and the tympanic ring of existing forms, like that of the *Testudinidæ*, is in great part closed behind. The nuchal bone of the carapace develops a long rib-like (costiform) process on either side, which underlies the marginals; and the complete union of the marginals with the costals does not take place for a long period; while in the plastron vacuities frequently persist till late in life, and the plastron itself may be relatively small, and unites with the carapace by gomphosis, the hyo- and hypoplastrals not giving off buttresses to underlie the carapace. In existing forms the caudal vertebræ are opisthocœlous; and there is no bony union between the ischium and pubis of the same side to enclose an obturator foramen. The head cannot be completely retracted within the shell. The humerus is not flattened, and has its radial and ulnar processes large, and directed towards the ventral aspect.

If all the genera provisionally included in this family are rightly referred, it will be the oldest representative of the order which still exists. The genera may be divided into three subfamilies, according to the presence or absence of sculpture or epidermal shields on the shell. It is, however, by no means certain that all these forms should be included in this family; but until we know the skull and caudal vertebræ of all the genera it is impossible to decide this point, and it may eventually prove that there is a more or less complete passage to the *Dermatemydidæ* from this family, since there already are some indications of a connection between them. Thus the American Cretaceous genus *Toxochelys* is stated by Dr Baur to be a true Chelydroid, but to have the procœlous caudal vertebræ

of *Dermatemys*, and also to have an open tympanic ring. The *Anostirinæ* are typically represented by *Anostira*, of the Upper Eocene of North America and England, and we may probably include in the same group *Pseudotrionyx* (*Apholidemys*), of the Middle and Lower Eocene of Europe. In these forms the shell has a vermiculated sculpture, but epidermal shields appear to be absent, although Dr Baur states there are traces of them in the typical genus; the plastron is well developed; and the neural bones are reduced to seven, as in *Dermatemys*. *Anostira*, which, on account of the presence of only ten marginal bones, Dr Baur places in the *Dermatemydidæ* (*Staurotypidæ*), differs from *Pseudotrionyx* by the sculpturing of the neural bones. The skull of *Pseudotrionyx*, originally referred by Sir R. Owen to *Platemys*, agrees essentially with that of *Macroclemmys*, although the orbits are less lateral. The second subfamily, *Tretosterninæ*, is represented by *Tretosternum*, of the English Wealden and Purbeck, with which *Peltochelys*, of the Wealden of Belgium, is identical. Possibly the imperfectly known North American Cretaceous genus *Compsemys* may prove to be a closely allied, if not identical, type. The shell is studded with granular tubercles, and has epidermal shields; while the plastron is larger than in the *Chelydrinæ*, and has an intergular shield. This is, however, accompanied by only five paired plastral shields, as in *Dermatemys*, instead of the six found in *Pleurosternum* (fig. 1012). The nuchal bone is deeply emarginate.

Finally, in the typical subfamily *Chelydrinæ* the shell is not sculptured, and has epidermal shields; the plastron is relatively small, and generally has a median vacuity; while there is the full number of eight neural bones, of which the last articulates with a suprapygal, and thus prevents any of the costals from meeting in the middle line. The type genus *Chelydra* is represented in the Puerco or Lowest Eocene of the United States, and also occurs in the Upper Miocene of Switzerland, the Middle Miocene of Styria (where it has been described as *Chelydropsis*), and the Lower Miocene of Rott, near Bonn. No fossil forms have hitherto been referred to *Macroclemmys*, which is distinguished from *Chelydra* by the more deeply emarginate nuchal, and the lateral orbits of the skull, which is very large in proportion to the shell and limb-bones.

Family Cinosternidæ.—With the American genus *Cinosternum* we come to a family readily distinguished by the total absence of the entoplastral element of the plastron. In the existing genus the skull has open temporal fossæ, the nuchal has a costiform process like that of the *Chelydridæ*, the pelvis is of a Testudinate type, and the caudal vertebræ are procœlous. The absence of the entoplastral also occurs in the Swiss Eocene genus *Dithyrosternum*, which has accordingly been placed in the same family. It is distinguished from

Cinosternum by the presence of eight neural bones, and the long bridge connecting the carapace with the plastron.

Family Dermatemydidæ.—The genus *Dermatemys*, of Central America, is taken as the type of a family which includes *Staurotypus* of the same region, and in some respects connects the *Cinosternidæ* with the *Chelydridæ*. The nuchal bone has a costiform process, as in both those families; the temporal fossæ of the skull are not roofed over; the caudal vertebræ are procœlous; and in the pelvis the pubis and ischium of the same side do not unite to enclose an obturator foramen. The shell is well ossified, but in the type genus the union between the costals and marginals does not take place till a late period. *Baptemys*, of the Upper Eocene of North America, which has been included by Professor Cope in *Dermatemys*, is distinguished from the latter by having the full number of neural and suprapygal bones, so that none of the costals meet in the middle line. Here may be mentioned several allied North American forms, most of which are referred by Professor Cope to a distinct family—the *Adocidæ*—mainly on account of the circumstance that the ribs do not develop heads to articulate with the vertebræ; but since the same feature occurs in *Testudo* among the *Testudinidæ*, it cannot be regarded as of family value. In *Homorophus*, of the American Cretaceous, there is no intergular shield, and the vertebral shields are very narrow. In *Adocus*, of the Upper Cretaceous, and *Agomphus* (with which Dr Baur states *Amphiemys* is identical), of the Eocene, intergular shields were present. The former has traces of sculpture on the shell; while in the latter the epidermal shields are very thin, and the surface of the shell is marked with a faint vermiculate sculpture. We are thus led on to the European *Trachyaspis*, which is probably an allied form, and with which one or other of the American types may perhaps prove to be identical. This genus, which has elongated vertebral shields recalling those of *Dermatemys* and *Baptemys*, occurs typically in the European Tertiary, and has also been recorded from the Lower Greensand of Switzerland, although the latter form has been referred by Professor Rütimeyer to *Plesiochelys*. A nearly entire carapace has also been obtained from the Tertiary of Egypt. The surface of the shell is covered with a distinct vermiculated sculpture like that of *Trionyx*, but thin epidermal shields were present.

Family Platysternidæ.—The existing Burmese genus *Platysternum* is represented by a very small Chelonian forming the only member of a family which connects the *Chelydridæ* with the *Testudinidæ*. Thus the temporal fossæ of the skull are roofed over, the pelvis is of a Chelydroid type, and the caudal vertebræ are mostly opisthocœlous; but the nuchal agrees with that of the *Testudinidæ* in having no costiform process.

Family Testudinidæ.—Following Mr Boulenger's arrangement, this extensive family is taken to include the *Cistudinidæ* and most of the *Emydidæ* of other writers, and may be briefly characterised as follows: The limbs terminate in free digits; epidermal horny shields are always present, but there is no intergular shield; the carapace is ovoid and fully ossified; the plastron in the adult is connected with the carapace either by suture or a straight articulation, and is always fully ossified. There is no costiform process to the nuchal bone; the temporal fossæ of the skull are not roofed over by bone; the caudal vertebræ are procœlous; and the pubis and ischium of either side unite to enclose an obturator foramen. The humerus has a well-developed head, and its shaft is more or less curved. The skull is of nearly equal width throughout its post-orbital portion. The Terrapins and Tortoises, as the existing members of this family are commonly termed, exhibit great variety of habits, some being aquatic and others terrestrial; while some, again, are carnivorous and others herbivorous. Some of the terrestrial forms have the normal two epidermal caudal shields of the carapace fused together into a single large shield.

We may commence our brief survey of this large family with the Oriental group of Batagurs, represented by *Batagur*, *Kachuga*, *Hardella*, and allied types. These include freshwater Terrapins, frequently of large size, characterised by the great development of the axillary and inguinal buttresses of the plastron, which divide the sides of the carapace into chambers, and also by the presence of one or more strong ridges on the oral surface of the palate, running parallel to its alveolar borders. On the plastron (fig. 1016) the sulcus between the humeral and pectoral shields is below the entoplastral. *Kachuga* (including *Pangshura*) has the fourth vertebral shield elongated, and overlying parts of four or five neural bones; the anterior neurals being elongated and hexagonal, with the short side anterior. The typical *K. lineata*, in which the fourth vertebral shield is broad anteriorly, is represented in the Pliocene Siwaliks of India, which also yield the existing *K. dhongoka*. In a second group (*Pangshura*), in which the fourth vertebral shield is narrowed to a point at its junction with the third, we have the existing *K. tectum* (fig. 1016) in the Pleistocene and Pliocene of India. *Hardella* (fig. 1017) is characterised by the shortness of the fourth vertebral shield, which usually extends over three neural bones (four in the figure), and by the third vertebral shield overlying parts of three (in place of two) neurals. It is represented in the Siwaliks by the existing *H. Thurgi* (fig. 1017). With the existing American genus *Chrysemys* we come to forms in which the axillary and inguinal buttresses are much less developed than in the Batagurs, and the neural bones are shorter than in *Hardella*.

In *Chrysemys* itself the sulcus between the humeral and pectoral shields of the plastron is situated entirely on the hyoplastral, as in fig. 1016; and from the presence of this feature, it is probable that the so-called *Emys testudiniformis* and *E. bicarinata*, of the London Clay, should be referred to this genus. In the existing genus *Ocadia*, from China, and also in the Palæarctic and North American *Clemmys*, the humeropectoral sulcus is placed somewhat more anteriorly, and consequently cuts the entoplastral bone. A similar feature is frequently found in the so-called *Emys crassa* (*hordwelliensis*), of the Upper Eocene of Hampshire; and it appears that this form should be referred to the genus *Palæochelys*, of the German Miocene, from which *Ocadia* is probably not separable. *Emys wyomingensis*, of the Upper Eocene of North America, appears to be referable to the same genus. *Ocadia*, it may be observed, agrees with the herbivorous Batagurs in the presence of ridges on the palate; but these ridges are absent in *Clemmys* and the undermentioned forms, which are purely carnivorous.

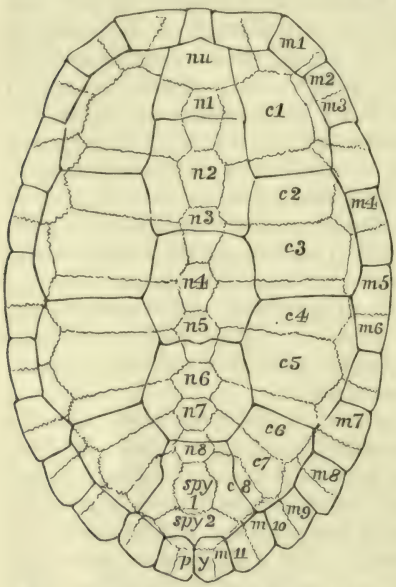

Fig. 1017.—Carapace of *Hardella Thurgi*; India. *nu*, Nuchal bone; *n1–n8*, Neural do.; *spy*, Suprapygal do.; *py*, Pygal do.; *c1–c8*, Costal do.; *m1–m11*, Marginal do. Reduced.

These forms may be divided into two groups, according as to whether the plastron is united to the carapace by suture, or simply by ligament. In the former series *Clemmys* is represented in the Pliocene of Algeria by a species closely allied to the existing *C. leprosa* of that region. The characteristic Oriental genera *Damonia* and *Bellia* are represented in the Pliocene Siwaliks of India; the fossil *Damonia* being apparently inseparable from the living *D. Hamiltoni*. In the second series, where there is a more or less complete transverse hinge in the plastron at the junction of the hyo- and hypoplastrals, and the buttresses of the carapace may be wanting, we find remains of the existing *Emys orbicularis* (*E. lutraria* or *Lutremys*), commonly known as the European Pond-tortoise, in the Pleistocene of England and the Continent. *Cistudo*,

which is almost exclusively terrestrial, has been recorded from the Continental Miocene. The Indian genus *Nicoria*, which is represented by the existing *N.* (*Chaibassia*) *tricarinata* in the Siwaliks, is distinguished from all the preceding forms in that the neural bones have their short side placed posteriorly. The extinct *Ptychogaster*, of the Lower Miocene (Upper Oligocene) of France, is characterised by the ligamentous junction of the hypoplastral with the carapace, and by the presence of a hinge between the hypo- and hyoplastrals, and also by the contour of the neural and costal bones, which approximate to those of the true Tortoises; from which we may assume that this form was mainly of terrestrial habits. In both genera the humero-pectoral sulcus cuts the entoplastral bone.

In the land Tortoises, forming the last group of the family, the neural bones are generally very short and wide, and may be either hexagonal, or alternately tetragonal and octagonal; while the costal bones are generally alternately short and long at their inner and outer extremities; the suture between the marginal and costal bones usually coincides with the sulcus dividing the corresponding shields, and the caudal shield is generally undivided. In most cases the sulcus between the humeral and pectoral shields is behind the entoplastral bone. The digits differ from those of most of the preceding genera by being adapted solely for walking, and devoid of webs; while the metacarpals are shorter, and the humerus is very much curved, with its radial and ulnar processes approximated. The least specialised existing forms are *Cynixis* and *Pyxis*, which have neural bones like those of *Homopus*, but costals of the ordinary Emydine type; they appear to be unknown as fossils. *Hadrianus*, of the Upper (Bridger) Eocene of the United States, includes generalised Tortoises of large size, in which the neural bones are elongated and hexagonal, with the shorter lateral surfaces posterior; the costals do not alternate in length; the vertebral shields are narrow; and the caudal shield is divided. The genus *Homopus*, which now includes a few species of small size confined to Africa, has no ridge on the palate, and the neural bones are short and hexagonal, with short postero-lateral surfaces, and the caudal shield is single. It is represented in the Upper Miocene of Switzerland by the so-called *Emys scutella*, and in the London Clay by *E. Comptoni*. In *Stylemys*, from the White River Miocene of the United States, the short neural bones have their shorter lateral surface placed anteriorly, the posterior costals do not alternate in length at their extremities, and there is a single caudal shield. All the remaining forms may be included in *Testudo*, in which the palate has one or two ridges; the neural bones usually consist of an alternation of small tetragonal and larger octagonal ones; while the anterior extremity of the epiplastrals is more or less thickened. In the skull the pterygoids are wide, and depressed

in the middle (fig. 1017 *bis*). Usually the caudal shield is single, but it may be divided. The ribs have no heads for articulation with the vertebræ. The forms described as *Manuria* and *Colossochelys* may be included in this genus, which comprises a large number of species. Exclusive of the Jurassic so-called *T. Stricklandi*, which has been already mentioned under the head of *Protochelys*, the earliest occurrence of the genus appears to be in the Upper Eocene Phosphorites of France; it is, however, not certain that the form from these deposits may not be referable to one of the American genera. A marginal in the British Museum indicates an individual about 30 inches in length. *T. gigas*, of the Miocene of Haute-Loire, is a still larger form; and species of large dimensions also occur in the Lower Miocene of Allier and the Middle Miocene of Gers, as well as in the Pliocene of France and Greece.

The huge *T.* (*Colossochelys*) *atlas*, of the Pliocene Siwaliks of India, was one of the earliest of the large extinct forms brought to the notice of science, although its size has been greatly exaggerated. It appears, indeed, that the length of the carapace was about six feet, or one-third greater than in *T. elephantina*, of the Galapagos Islands. This species is remarkable for the great development of the epiplastral bones, which formed a pair of horn-like processes; and is also noteworthy for the anchylosis of the three bones of the pelvis into an innominate bone. The skull, which probably belongs to this species, resembles in structure the skulls of the recent giant tortoises of Aldabra. The carapace had no nuchal shield, the caudal shield was divided, and the limbs were covered with bony ossicles, as in the existing *T. emys* of India, to which this form was probably allied. The large *T. perpiniana*, of the Pliocene of France, in which the depressed carapace measures nearly four feet in length, and the limbs were likewise covered with dermal ossicles, was probably also nearly allied. An unnamed species, from the Pliocene of the Siwalik Hills, has a skull resembling that of the Galapagos tortoises (fig. 1017 *bis*); which are characterised by the backward extension of the opisthotics. We also find in the Siwaliks *T. Cautleyi* characterised by its small epiplastrals; and *T. punjabiensis*, which appears to have been a form allied to the smaller existing Indian *T. emys*. Remains of giant tortoises also occur in the Pleistocene cave-deposits of Malta.

Finally, we must not omit to briefly mention the giant tortoises of the present epoch, which, it appears, have been driven from the continental areas by the competition of the higher types of life to seek refuge in islands, where they attained an extraordinary numerical development, till their haunts were invaded by man. These tortoises formerly existed in great numbers in the islands of the Aldabra group, lying to the north-west of Madagascar; in the Mascarenes, which comprise Mauritius and Rodriguez; and also in the Galapagos, or "Tortoise-Islands," which lie off the coast of South America. The Aldabra Tortoises are characterised by their deeply excavated palate, short opisthotics, and the presence of a nuchal and of double gular shields. Some of them were living in the year 1877. In the Pleistocene of Madagascar remains of two very large species have been found, both of which present the characters of the Aldabra forms. The Mascarene species have no nuchal shield, and only a single gular; and the whole of them have been exterminated by human

agency. Their skulls resemble those of the next group (fig. 1017 *bis*) in the slight excavation of the palate, and the produced opisthotics. Finally, the Galapagos tortoises, a considerable number of which were found in Albemarle and Abingdon Islands during the voyage of the Challenger, are distinguished by the double gulars and the absence of the nuchal shield. From the Pleistocene of South America, Dr Moreno describes two large tortoises allied to the Galapagos forms; one of them being

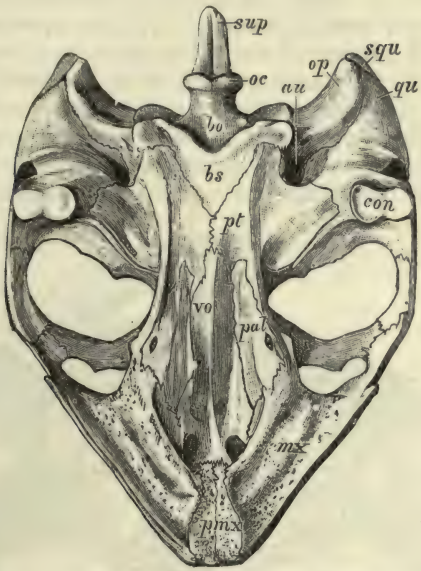

Fig. 1017 *bis*. — Palatal aspect of the cranium of *Testudo microphyes;* from the Galapagos Islands. Two-thirds natural size. *au*, Auditory aperture; *bo*, Basioccipital; *bs*, Basisphenoid; *con*, Condyle of quadrate; *mx*, Maxilla; *oc*, Occipital condyle; *op*, Opisthotic; *pal*, Palatine; *pmx*, Premaxilla; *pt*, Pterygoid; *qu*, Quadrate; *squ*, Squamosal; *sup*, Supraoccipital spine; *vo*, Vomer.

described as the probable ancestor of *T. nigra* (*elephantopus*) of the latter group. The carapace of *T. elephantina* measures four feet in a straight line.

Family Chelonidæ.—The last family of the Cryptodira differs from all the preceding in having the limbs modified into more or less complete paddles or flippers (fig. 1018), which in the existing forms have only one or two claws. The carapace is broad and more or less depressed, and is very generally heart-shaped (fig. 1018), although in some of the early forms it is rounded at both extremities. The nuchal bone has no costiform process; there are usually larger or smaller unossified spaces between the costals and marginals of the carapace (fig. 1006), but in very old individuals these may obliterate in some forms; and the plastron is not articu-

lated to the carapace, and has digitated lateral terminations, and generally a larger or smaller median vacuity (fig. 1009). The humerus is more or less flattened, with the axis of the head generally placed nearly immediately above that of the shaft, and the radial process small, and placed more or less below the well-developed head. The caudal vertebræ are procœlous, and the cervicals extremely short. In the skull the temporal fossæ are completely roofed over by bone, so that the squamosal joins the parietal; and the bones of the palate unite for a longer or shorter distance beneath the narial passage, so as to throw the posterior nares more or less backward (fig. 1020). The prefrontals (as in most *Testudinidæ*) always form a re-entering angle posteriorly; and the tympanic cavity is quite open posteriorly, so as to expose the stapes. In old individuals the vacuities in the shell tend to ob-

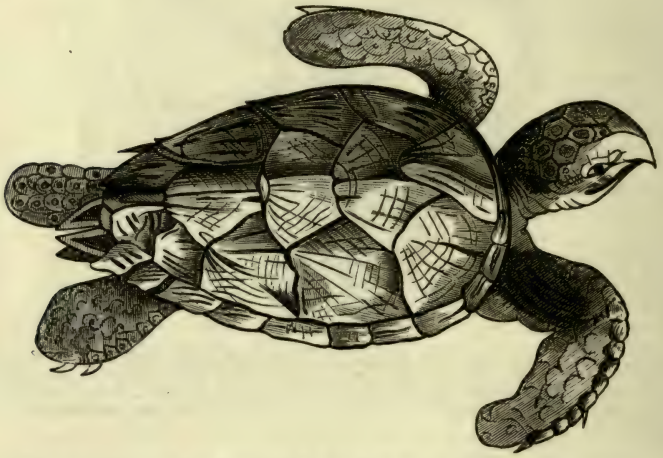

Fig. 1018.—Young of the Hawksbill Turtle (*Chelone imbricata*). Much reduced. (After Bell.)

literate, and in the more generalised extinct types this tendency is much more marked, and it is quite probable that in some cases they may have completely disappeared. This more complete ossification of the shell in these generalised types indicates affinity with the preceding families, and probably more especially with the *Acichelyidæ;* and the same is indicated by other features, such as the more marked constriction of the shaft of the humerus, and the more oblique position of its head, together with the probable presence of claws to all the digits. Some writers, indeed, consider these more generalised types as entitled to constitute a distinct family—the *Propleuridæ;* but their close relationship to the existing Log-

gerhead forbids this view. We have already suggested reasons for regarding this family as being descended from the Mesozoic *Aci-chelyidæ*, and from this point of view it is interesting to note the presence of an intergular shield in the plastron of the existing, and probably, therefore, of the fossil forms, since, as we have already stated, this appears to be an archaic feature. The same observation will apply to the open tympanic ring. At the present day there are four living species of Turtles — viz., the Loggerhead (*Thalassochelys caretta*, fig. 1006), the Mexican Loggerhead (*T. Kempi*), the Hawksbill (*Chelone imbricata*, fig. 1018), and the Green Turtle (*C. mydas*), all of which are of purely marine habits. The Hawksbill alone is carnivorous; and is further peculiar for the circumstance that in the young state the epidermal shields imbricate, instead of uniting by their edges. It has been suggested that the extinct genera were of estuarine rather than purely marine habits; and this is borne out by their occurrence in the estuarine deposits of the London Clay, to the exclusion of the marine genus *Chelone*.

The most remarkable of the extinct genera is *Lytoloma* (*Euclastes*, *Puppigerus*, *Glossochelys*, or *Erquelinnesia*), which occurs typically in the Eocene of North America and the London Clay, and is also represented in the Middle Eocene of Bracklesham, as well as in the Chalk and Cambridge Greensand. In the typical Eocene forms, like the so-called *Chelone planimentum* and *C. crassicostatum* of the London Clay, the skull is as large in proportion to the shell, as in *Macroclemmys* among the *Chelydridæ*. The skull of the adult is remarkable for the extremely backward position of the posterior nares, which are approximated to the basioccipital; and for the length and width of the mandibular symphysis (fig. 1019, A). The palate has low alveolar walls, and no oral ridge; the nares and orbits are directed somewhat upwardly; and the bar between the latter is narrow. The shell is characterised by the great extent of its ossification, as well as by the rounded posterior extremity of the carapace, and the sutural connection of the broad xiphiplastrals in the median line. The head of the humerus is somewhat oblique, and its shaft much constricted. The limbs were clawed. Curiously enough, in the young, and perhaps also in the adult of some of the smaller forms, the posterior nares were placed much less backwardly, and the mandibular symphysis was shorter and less flattened. It is probable that at least some of the North American Eocene forms described as *Osteopygis*, *Propleura*, and *Catapleura*, are not separable from this genus; while a turtle from the Cretaceous of Australia, originally described by the preoccupied name of *Notochelys*, but which has been provisionally designated *Notochelone*, is probably also nearly related.

Closely allied to the preceding is the genus *Thalassochelys*, as represented by the Loggerhead (fig. 1006). The skull is, however, relatively smaller in proportion to the shell, which is distinguished by the presence of five costal shields; the carapace is heart-shaped; the xiphiplastrals are narrow, and join only at their extremities; while the terminal phalangeals are flattened and have but one or two claws. The shell is distinguished from that of *Chelone* by its more complete ossification, and its T-shaped entoplastral; while

Fig. 1019.—Oral aspect of the left half of the mandible of *Lytoloma crassicostatum* (A), and *Chelone mydas* (B). Reduced. The former from the Lower Eocene of Belgium, the latter recent. *e*, Postarticular process; *o*, Splenial; *n*, Geniohyoid groove; *g*, *k*, Insertion of temporal muscle; *h*, Coronoid process.

the humerus is more constricted, and has its head placed more obliquely. The position of the posterior nares and the form of the palatal walls and mandibular symphysis closely resemble the same parts in the young of *Lytoloma*. In very old specimens the vacuities between the costals and marginals completely close up. This genus probably occurs in the London Clay,[1] and also in the Middle Eocene of Bracklesham.

[1] As indicated by a mandibular symphysis in the British Museum.

In *Argillochelys*, of the London Clay, the skull (fig. 1020), which is very short and has deeply emarginate pterygoids, differs from that of the preceding genera by the presence of an oral ridge on either side of the palate and in the middle of the mandibular symphysis, although these are present in the Mexican Loggerhead. The vomer, as in the young of *Lytoloma*, is very long, and extends forwards to join the premaxillæ; and the pterygoids are characterised by the forward position of their ectopterygoid processes. The shell seems to have been much like that of *Thalassochelys*, but had only four costal shields, and its plastron was perhaps

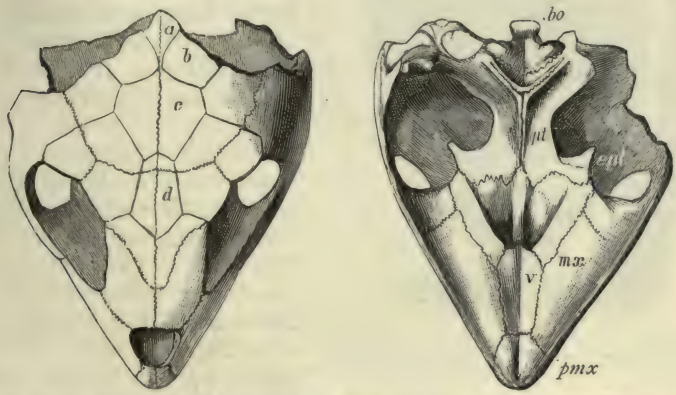

Fig. 1020.—Frontal and palatal aspects of a young cranium of *Argillochelys cuneiceps*; from the London Clay. Owing to immaturity the palatal ridges are imperfectly developed. *a*, Occipital, *b*, Paroccipital, *c*, Parietal, and *d*, Frontal epidermal shields; *bo*, Basioccipital; *pt*, Pterygoid; *ept*, Ectopterygoid process of do.; *v*, Vomer; *mx*, Maxilla; *pmx*, Premaxilla. The bones on the frontal aspect correspond with those of fig. 1022, in which letters are given.

less ossified, although the xiphiplastrals united extensively in the middle line. The mandibular symphysis is convex, and comparatively short. The skull of the type species was originally described as *Chelone cuneiceps*; while the shells figured as *C. subcristata* and *C. convexa* are referable to this genus.

In the typical genus *Chelone* the skull is much smaller in proportion to the shell than in *Thalassochelys*. It is characterised by the more or less nearly vertical position of the nares and orbits, and the width of the bar between the latter; by the tall alveolar walls and the oral ridges of the palate and mandibular symphysis; the long pterygoids, with the ectopterygoid processes placed somewhat backwardly; the forward position of the posterior nares; and the more or less marked shortness of the convex mandibular symphysis (fig. 1019, B). The skull, moreover, has no occipital epidermal shield, which is generally present in the other forms (fig. 1020). In the

shell the carapace is either heart-shaped, or pointed at each end (fig. 1021); the vacuities are large and persistent; the entoplastral is long and dagger-shaped; and the xiphiplastrals are slender and separate (fig. 1009). The humerus is but little constricted, with its head nearly on the axis of the shaft; and the coracoid is longer and more slender than in *Thalassochelys;* the Green Turtle (*C. mydas*) being more specialised in these respects than the Hawksbill (fig. 1018). The earliest occurrence of the genus appears to be in the Cambridge Greensand and Gault, where *C. Jessoni* has a very massive mandible, somewhat resembling that of the Hawksbill. This form may possibly be identical with *C. Benstedi* of the Chalk (fig. 1021), which is only definitely known by very young shells, and has been made the type of the genus *Cimoliochelys*. In the topmost Cretaceous of Maastricht the gigantic *C. Hoffmanni* appears to be allied to *C. imbricata*, but has a shorter and wider palate and mandibular symphysis, a more deeply emarginate nuchal, and the costal bones extremely short. From the latter very specialised character Dr Baur regards this species as entitled to generic distinction, and has proposed the name of *Allopleuron*. An equally large, and perhaps closely allied turtle occurs in the English Chalk. In the higher Miocene of Bordeaux *C. girondica* appears to be a form closely allied to existing types.

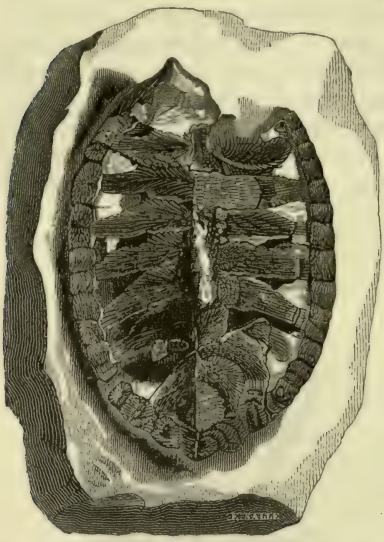

Fig. 1021.—Carapace of *Chelone* (?) *Benstedi;* from the English Chalk. Reduced. (After Owen.)

Section 4. Trionychoidea.—The last section of the suborder includes the mud-turtles or soft-tortoises, of the freshwaters of Asia, Africa, and North America; all of which are of aquatic and carnivorous habits. These forms, which may probably be regarded as extremely specialised types, present the following distinctive features. The shell is sculptured and devoid of epidermal shields; its entoplastral being in the form of a chevron, which divides the epiplastral from the hyoplastral; and the marginals, if present, forming only an incomplete series at the posterior extremity of the carapace, and having no connection with the ribs. The long cer-

vical vertebræ have no distinct transverse processes, and the eighth articulates with the first dorsal solely by the zygapophyses, thus forming the most remarkably complete hinge-joint among the whole of the Vertebrata. The fourth digit in each limb is characterised by having not less than four phalangeals. The form of the tympanic ring of the quadrate, and the relations of the latter to the mandible, are of the same type as in the Cryptodira; and we find a similar absence of union between the pelvis and the plastron. In the cranium (fig. 1022) the chief distinctive features are to be found in the palate; thus the broad pterygoids are separated from one another by the basisphenoid, which extends forwards to join the palatines; the latter, owing to the small size of the vomer, uniting extensively in the middle line; and the whole structure of the palate being of a Pleurodiran type. As minor characters of the skull, attention may be directed to the open temporal fossæ, and the forward position and upward direction of the small orbits, as well as to the extreme development of the backward processes of the supraoccipital and squamosal. The sacral and caudal ribs articulate only with the arches of the vertebræ, and there are no chevrons. The plastron is always entirely separate from the carapace, and has a large median vacuity and digitate extremities, as in the marine *Chelonidæ*. Further, the head and neck are retracted within the carapace after the Cryptodiran manner, but, owing to the peculiar structure of the eighth cervical vertebra, in a still more complete way. In all cases the posterior lateral surfaces of the neural bones of the carapace are much shorter than the anterior.

The marked resemblance of the palate and the general aspect of the Trionychoid skull to that of existing Pleurodira is a circumstance that does not admit of a ready explanation from a phylogenetic point of view, unless we adopt the somewhat improbable suggestion that the Pleurodira gave origin to the Trionychoidea at a time when their pterygoids had attained their full width, but while the tympanic ring was still partially open.

Family Trionychidæ.—The whole of the members of this section may be included in a single family, which is, however, susceptible of division into two subfamilies. In the first, or *Emydinæ*, the opisthotic of the skull unites with the pterygoid to divide the posterior aperture of the auditory labyrinth into two foramina; the hyo- and hypoplastral of either side are fused together; the sculpture of the carapace is tuberculated; and marginals may be present. The existing Oriental genus *Emyda*, in which marginals and a complete series of neurals are present, is represented by numerous species in the Pliocene Siwaliks of India, some of which attained very large dimensions. The African genera *Cyclanorbis* and *Cycloderma*, in which marginals were not developed, are at present unknown in a

fossil state. In the second subfamily, or *Trionychinæ*, the hyo- and hypoplastrals remain distinct throughout life; the pterygoid does not join the opisthotic behind the labyrinth; the sculpture usually consists of sinuous ridges or pits; and marginal bones are never developed in the carapace. The type genus *Trionyx* is widely distributed at the present day, and extends downwards into the Lower Eocene of both Europe and the United States, and is also represented in the Upper Cretaceous of the latter area. Many species are remarkable for showing dimorphic types of skull, which in one modification has a broad palate adapted for crushing, while in the other the palate is very narrow. The Indian species, in which the skulls are not subject to this variation, have two short neural bones between the first costals; while in the recent American forms there are but seven pairs of costals. All the European fossil forms agree with the majority of species in having only one long neural bone between the first costals. In Europe this genus appears to be unknown above the Upper Miocene of Œningen, and it is extremely abundant in the Upper Eocene (Lower Oligocene) of Hordwell. The existing Indian species occur in the Pleistocene and Pliocene of that country. Of the American Tertiary species at least some have eight costals, and in some cases only six neurals. The Lower Eocene and Upper Cretaceous forms described by Professor Cope as *Plastomenus* may be included in the type genus, since the thickening of the plastron can scarcely be regarded as a generic character. The same remark applies to the Eocene *Axestus*, of the United States, in which the plastron is smooth, as in some existing forms. An apparently distinct type, in which the outer margin of the costals is deeply grooved, occurs, however, in the English Upper Eocene, which has been named *Aulacochelys*. Finally, the exclusively Oriental genus *Chitra* is represented in the Pliocene and Pleistocene of India by remains of the one existing species *C. indica*, the largest member of the family.

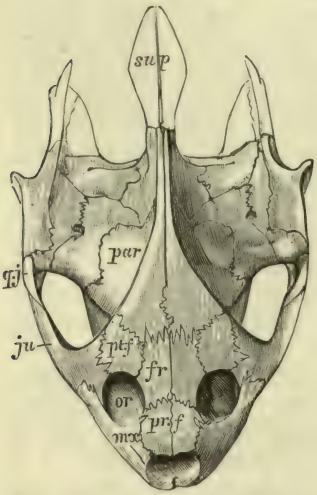

Fig. 1022.—Frontal aspect of the cranium of *Trionyx gangeticus*; from the Pleistocene of India. Reduced. *sup*, Supraoccipital; *par*, Parietal; *pt.f*, Postfrontal; *fr*, Frontal; *prf*, Prefrontal + nasal; *mx*, Maxilla; *ju*, Jugal; *q.j*, Quadratojugal; *or*, Orbit. The processes on either side of the supraoccipital are formed externally by the squamosal, and internally by the opisthotic, of which the inner border articulates with the supraoccipital; externally to the parietal is the proötic.

CHAPTER LIV.

CLASS REPTILIA — continued.

Orders Ichthyopterygia, Proterosauria, Rhynchocephalia, and Squamata.

Streptostylic Branch. — According to the arrangement proposed by Dr Baur, this branch is taken to include the four orders mentioned in the heading of this chapter. These orders present a remarkable instance of the divergent views obtaining among different writers as to the classification of Reptiles. Thus Professor Cope has proposed to place the Ichthyopterygia in a group by themselves, which he regards as of equal value to another containing all the other orders; while Professor Seeley at one time regarded this order as a division of the Dinosauria, although its relationship to the Squamata had been long before pointed out by Sir R. Owen. Professor Seeley has also proposed to separate the Squamata from all other Reptiles under the name of Cœnosauria, and to include the Rhynchocephalia in a second division as Palæosauria. Professor Cope, while not going so far as this, places the Rhynchocephalia in the Synaptosaurian branch; while Professor Huxley would include both that group and the Proterosauria in the Squamata (Lacertilia), from which the Ophidia are excluded. Dr Baur, again, merges the Proterosauria in the Rhynchocephalia, and regards the latter as a distinct order allied to the Squamata. This middle course is followed in the present work, although the Proterosauria, in accordance with the views of Professor Seeley, are provisionally allowed to rank as an order.

The present branch may be collectively characterised as follows: The dentition is very generally either acrodont or pleurodont, with the teeth of the adult anchylosed to the jaws; but the teeth may be implanted in a groove, and remain free. In addition to their presence in the jaws, teeth may also be developed on the palatine and pterygoid, and very rarely on the vomer. There is very fre-

quently a parietal foramen; the superior temporal arcade is generally present, but in the more specialised forms the inferior is often wanting. The quadrate may be either movably or immovably attached by its proximal extremity to the cranium; a columella is very generally present; and the ramus of the mandible never has a lateral vacuity. The precoracoid appears to be fused with the coracoid, and may be represented by a precoracoidal process (fig. 1040), or its position indicated merely by a fontanelle, while in the Ichthyopterygia even the latter is wanting. A T-shaped interclavicle and clavicles are present in all the earlier and a large proportion of the later forms. Usually all, or nearly all, of the dorsal ribs articulate by single heads; the dorsal vertebræ either have short or rudimental transverse processes, which are never placed entirely on the arch, or (Ichthyopterygia) a pair of facets on the centrum; and, with one exception, there are not more than two vertebræ in the sacrum. Abdominal ribs are present in the earlier, but are lost in most of the later forms. The humerus frequently has an ectepicondylar foramen. The number of phalangeals in the digits of pentedactylate land forms is generally 2, 3, 4, 5, 3, in the manus, and 2, 3, 4, 5, 4 in the pes.

In no case are secondary posterior nares formed by the development of plates from the bones of the palate to floor the narial passage; the posterior nares consequently always forming more or less slit-like horizontal apertures in the roof of the mouth. Neither is the posterior extremity of the palate ever completely closed by the junction of the pterygoids with the basisphenoid, after the fashion obtaining in the Chelonia (fig. 1017 *bis*) and some Sauropterygia; there being always a vacuity between the hinder extremities of the pterygoids which displays the presphenoidal rostrum.

Order IV. Ichthyopterygia.—The Mesozoic Ichthyosaurs and their allies were large marine Reptiles, with the body long, and shaped somewhat like that of the Cetacea (fig. 1023), without

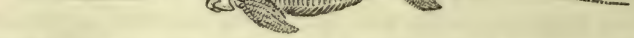

Fig. 1023.—Greatly reduced restoration of the skeleton of *Ichthyosaurus communis;* from the Lower Lias of Dorsetshire. The pelvic limb is relatively too large. (After Owen.)

either dermal or epidermal skeleton; the limbs being modified into paddles, in which the component bones were in apposition on all sides, and the phalangeals were oval or polygonal, and increased beyond the normal number. The skull (fig. 1024) has the facial region produced into a long rostrum, mainly formed by the pre-

maxillæ in the upper jaw; and the nares are consequently approximated to the orbit, which is of very large size, and has a ring of bony plates in the sclerotic; there is a large parietal foramen; and there are two temporal arcades connected together by the supratemporal (prosquamosal or supraquadrate), which roofs over the infratemporal fossa, after the Labyrinthodont fashion. Other char-

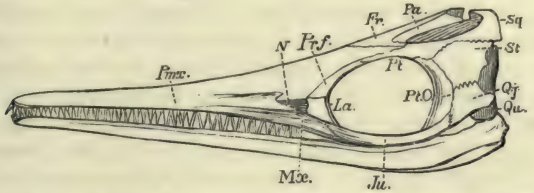

Fig. 1024.—Reduced left lateral view of the skull of *Ichthyosaurus intermedius;* from the Lower Lias of Dorsetshire. *Pmx*, Premaxilla; *Mx*, Maxilla; *N*, Nares; *La*, Lachrymal; *Prf*, Prefrontal; *Fr*, Frontal; *Pa*, Parietal; *Pt*, Postfrontal; *St*, Supratemporal; *Sq*, Squamosal; *Qj*, Quadratojugal; *Qu*, Quadrate; *Ju*, Jugal; *Pt.O*, Postorbital. (After Huxley.)

acteristic features of the skull are the small frontals; the presence of an opisthotic in the occipital region; the distinctness of the postorbital from the postfrontal, and of the lachrymal from the prefrontal; the firm fixture of the quadrate, which does not, however, suturally unite with the pterygoid; and the presence of a foramen separating the middle portion of the quadratojugal from that bone, as

Fig. 1025.—The centrum of an anterior dorsal vertebra of *Ichthyosaurus*, viewed in section, and from the anterior and left lateral aspects; from the Kimeridge Clay of Wiltshire. Reduced. (After Owen.)

in the existing Rhynchocephalian genus *Sphenodon*, and the presence of a columella, or epipterygoid. The palate has essentially the same structure as in the last-named genus. As in the Squamata, there is no lateral vacuity in the mandibular rami. The teeth are confined to the jaws, and are implanted in a continuous groove, without anchylosis to the bone. Their crowns are sharply pointed, and are usually

cylindrical and deeply fluted (fig. 1032), but are occasionally compressed, carinated, and smooth (fig. 1028). The vertebral column is primarily divisible only into a precaudal and a caudal series, there being no sacrum. The centra (fig. 1025) are amphicœlous, more or less disk-like, and either deeply cupped or nearly flat. On either side those of the precaudal series (fig. 1025) carry a pair of tubercles for the articulation of the double-headed ribs; while in the caudal region these tubercles coalesce. Superiorly each centrum has a pair of flattened surfaces for the attachment of the neural arches, which are united merely by synchondrosis. In the cervical region the tubercles for the ribs are placed near the summit of the lateral surfaces of the centra, and they gradually descend on the centrum, till they reach the base of the lateral surface in the posterior precaudal and caudal regions. In some forms the upper costal tubercle of the anterior vertebræ is placed either partly or entirely on the neural arch, and it is convenient to term such vertebræ, or their homologues, cervicals, and the remainder of the precaudal series dorsals. The centrum of the atlas vertebra is well developed, and

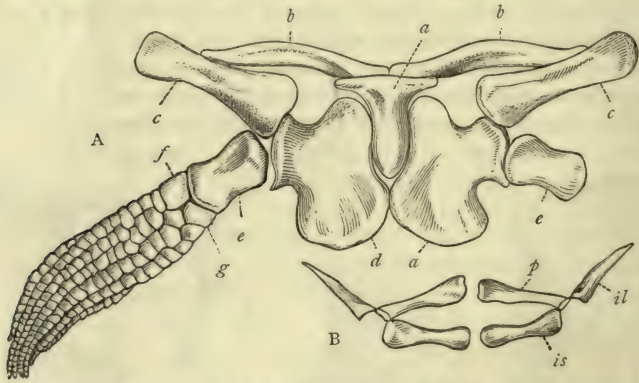

Fig. 1026.—A, Ventral aspect of the pectoral girdle and right limb of *Ichthyosaurus intermedius*. B, Pelvic girdle of do. Reduced. *a*, Interclavicle; *b*, Clavicle; *c*, Scapula; *d*, Coracoid; *e*, Humerus; *f*, Ulna; *g*, Radius; *il*, Ilium; *is*, Ischium; *p*, Pubis. (After Huxley.)

there is a large intercentum between the atlas and the skull, and another between the former and the axis. There was no sternum; but a complex system of abdominal ribs was developed. The dorsal ribs were devoid of uncinate processes; and ribs occur in the caudal region. In the pectoral girdle (fig. 1026, A) there is no precoracoid; but clavicles and a T-shaped interclavicle, like the corresponding bones of the Lacertilia, were developed. The coracoids were large and expanded, devoid of any fontanelle, and not

overlapping one another at their junction. The three bones of the pelvis (fig. 1026, B) are weak and rod-like; the ilia have no connection with the sacral region of the vertebral column; and although the pubis and ischium of opposite sides meet in the middle line, those of the same side do not unite to enclose the obturator notch. The humerus and femur are relatively short; but the radius and tibia are still shorter, and may be reduced to oblong bones in which the transverse diameter is the longer. The humerus has no foramen. The structure of the paddles will be noticed under the head of the different genera; but it may be observed that when there is a difference in the size of the limbs it is the pectoral that is the larger. From the less specialised structure of the limbs of the earlier forms Dr Baur regards the Ichthyopterygia as descendants of land animals; a conclusion which is supported by the argument that had these Reptiles originated directly from Fishes, as was formerly supposed to be the case, they would have retained their gills. In regarding this order as closely allied to *Sphenodon*, Dr Baur lays stress upon the general similarity in the cranial structure, and especially the presence of the foramen between the quadrate and quadratojugal; the identical structure of the abdominal ribs; and the remarkable similarity of the pectoral girdle, which, this author remarks, is only comparable to that of the existing genus, especially when young. In the skull and vertebral column the Ichthyopterygia retain evidences of their Labyrinthodont descent, which are lost in the other orders of this branch.

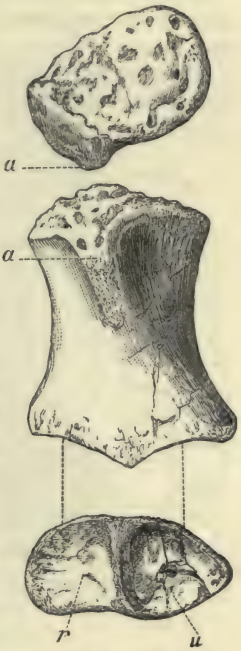

Fig. 1026 *bis.* — Proximal, dorsal, and distal aspects of the left humerus of *Ichthyosaurus*; from the Kimeridge Clay. One-third natural size. *a*, Trochanteric ridge; *r*, Facet for radius; *u*, Do. for ulna.

This order is known to range with certainty from the Upper Trias to the Upper Chalk. It was also widely distributed in space; its remains having been discovered in the Arctic regions, in Europe, India, Ceram, North America, the east coast of Africa, Australia, and New Zealand. Part of a jaw referred to *Ichthyosaurus* has been described from Malta, which, it has been suggested, may be of Miocene age, but this requires confirmation.

It may be remarked that the humerus and femur of this order are quite unique in that, instead of having convex condyles for the

articulation of the epipodial bones, they present distinct concavities (fig. 1026 *bis*) for their reception.

Family Ichthyosauridæ.—Although Dr Baur makes the genera *Mixosaurus*, *Ichthyosaurus*, and *Opthalmosaurus* the types of as many families, yet it seems on the whole more convenient to include all the known forms in a single family. The most generalised group with which we are at present acquainted is the genus *Mixosaurus*, from the Upper Trias of Italy, which is founded upon a small species presenting the following characters. The humerus and femur articulate distally with two bones; and the radius and ulna are elongated, and separated from one another by an interval throughout their entire length. The teeth are small, and not excessively numerous. It may eventually prove that all the Triassic forms are referable to this genus. The type genus *Ichthyosaurus* is characterised by the usual presence of teeth throughout the jaws; and by the normal articulation of the humerus with only the short radius and ulna, which are in close apposition (fig. 1027). In the pelvic limb the femur similarly articulates only with the tibia and fibula at its distal extremity; and thus this extremity in both the humerus and femur has only two articular facets (fig. 1026 *bis*). The bone which articulates inferiorly with the radius and ulna at their junction is the intermedium (fig. 1027, *i*); while the one filling up the angle between the latter and the radius is the radiale; the opposite angle being occupied by the ulnare. Below the intermedium we have the centrale, which in the more specialised forms may be double (fig. 1031), and below this the remaining carpals, metacarpals, and phalangeals, which are combined to form a pavement-like structure. The bones forming the continuation of the line of the intermedium in fig. 1027 correspond to the middle or third digit of the typical manus; and the structure of this limb indicates that it was derived from a four-fingered ancestor, since the pollex, or first digit, is not represented.

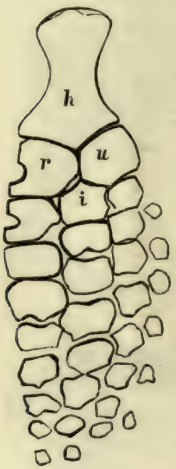

Fig. 1027. — Dorsal aspect of the left pectoral limb of *Ichthyosaurus latifrons*; from the Lower Lias. Reduced. *h*, Humerus; *r*, Radius; *u*, Ulna; *i*, Intermedium. (After Owen.)

Specimens have been obtained from the Lias of Würtemberg and Barrow-on-Soar, in Leicestershire, which show the contour of the integuments of the paddles. It appears from these that on the anterior border of the paddle (fig. 1027 *bis*) there was a comparatively narrow band of integument, which was covered by minute horny scales; while on the posterior border there was a much broader flap, which appears

to have contained parallel bands of muscles set obliquely to the axis of the paddle. In the Latipinnate group (fig. 1027 *bis*) the posterior flap of integument was narrow in proportion to the bony framework of the paddle, and it was produced inferiorly into a long point below the distal bones. In the Longipinnate group, however, the integuments were much wider in proportion to the bones, and they terminated inferiorly in a blunt extremity, which only reached a short distance below the distal bones.

The larger forms attained a length of from thirty to forty feet; and it is thought probable that the extremity of the tail was provided with a membranous fin. All the species were carnivorous; and, as we learn

Fig. 1027 *bis*.—Part of the left pectoral limb of *Ichthyosaurus intermedius*, viewed from the ventral aspect, and showing the contour of the integument. One-half natural size. *hu*, Humerus; *r*, Radius; *u*, Ulna; *r'*, Radiale; *i*, Intermedium; *u'*, Ulnare; *c*, *c'*, Centralia. From the Lower Lias of Barrow-on-Soar.

from the so-called coprolites, their food consisted to a considerable extent of Ganoid Fishes. These coprolites further tell us that the intestine was provided with a spiral valve, as in the Selachian fishes. Perhaps, however, the most remarkable circumstance connected with their internal economy is the not unfrequent occurrence of entire skeletons of small individuals within the thoracic and abdominal cavity of larger ones; these small specimens being invariably uninjured, and belonging to the same species as the one in which they are contained. This leads Professor Seeley to conclude that some species or individuals were viviparous, and that the young were probably produced of different relative bulk in different species. There is also evidence to show that in some cases many young were produced at a birth; the number being perhaps a specific character. It cannot, however, be taken as proved that all Ichthyosaurs were viviparous, since in such other Sauropsida and Ichthyopsida in which the same mode of development occurs, it is not distinctive of any entire group; and it is noteworthy that the three specimens

with young figured by Professor Seeley all belong to a single species. This genus may be divided into two groups from the structure of the pectoral limb. In the *Longipinnate*, or least specialised group, which is unknown above the Lias, the orbit is generally of very large dimensions. The pectoral limb (fig. 1027) is characterised by having the third digit, or that arising from the intermedium, comprising only a single longitudinal row of bones, and consequently having only one centrale; while there are usually only four longitudinal rows of phalangeals in this limb, and the radius is nearly square, with a distinct notch in its anterior border (fig. 1027). This group may be further subdivided into minor groups. One of the most aberrant forms is the huge *I. platyodon*, of the Lower Lias, which attained a length of nearly forty feet. This species is characterised by the pelvic paddles being nearly as large as the pectoral; but still more readily by the teeth (fig. 1028), which have compressed, carinated, and smooth crowns, and the roots covered with a coating of cement. *I. lonchiodon* is an allied Lower Liassic form with cylindrical and fluted teeth. Another type is indicated by *I. tenuirostris* and *I. latifrons* (*longirostris*), in which the cranial rostrum (fig. 1029) is greatly elongated and very slender. The paddles (fig. 1027) are remarkable for the large size of the component bones; and in *I. tenuirostris* there is a small circular vacuity between the radius and ulna, indicating the last remnant of the large vacuity found in *Mixosaurus*. Lastly, *I. acutirostris*, *I. zetlandicus*, and *I. integer* are three Upper Liassic members of this group indicating a transition to the next group; the radius of the latter species having no anterior notch. The skull of *I. zetlandicus* is shown in fig. 1030.

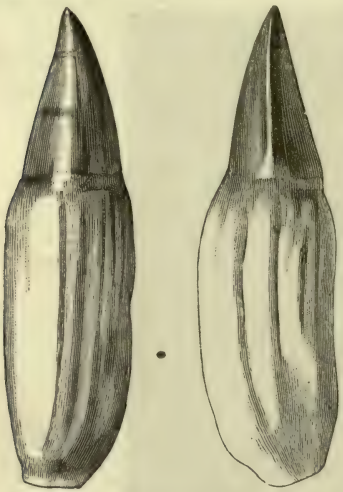

Fig. 1028.—Lateral and profile views of a tooth of *Ichthyosaurus platyodon*; from the Lower Lias of Dorsetshire.

In the more specialised or *Latipinnate* group, which ranges from the

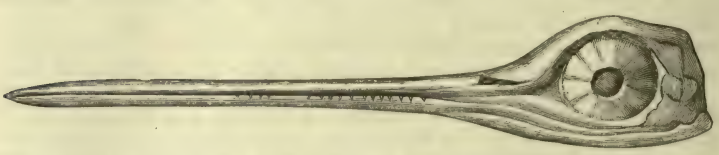

Fig. 1029.—Left lateral view of the skull of *Ichthyosaurus latifrons*; from the Lower Lias of Leicestershire. Reduced.

Lias to the Chalk, the orbit is usually relatively smaller than in the last group. The pectoral limb (fig. 1031) has the third digit, or that arising from the intermedium, with a double longitudinal row of bones, and there are consequently two centralia. There are, moreover, never less than

five longitudinal rows of phalangeals in this limb (the marginal rows are wanting in fig. 1031); and the radius is transversely elongated (and thus very widely removed from the normal type) with an entire anterior border. It is important to observe that in this group the splitting of the third digit and the two centralia are evidently acquired, and not inherited characters. Like the last, this group may be divided into subgroups. In the typical subgroup, which is confined to the Lias, the teeth (fig. 1032) have their roots strongly fluted, and the dorsal aspect of the humerus has no strongly-marked trochanteric ridge. *I.*

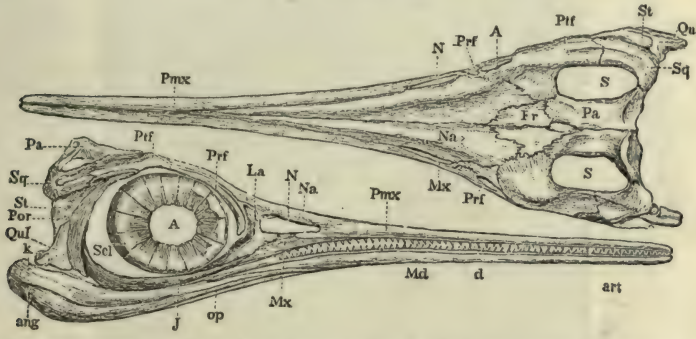

Fig. 1030.—Superior and right lateral aspects of the skull of *Ichthyosaurus zetlandicus*; from the Upper Lias of Caen. Reduced. *Pmx*, Premaxilla; *Mx*, Maxilla; *N*, Nares; *Na*, Nasal; *La*, Lachrymal; *Prf*, Prefrontal; *Fr*, Frontal; *Pa*, Parietal; *Ptf*, Postfrontal; *Sq*, Squamosal; *St*, Supratemporal; *Por*, Postorbital; *QuJ*, Quadratojugal; *J*, Jugal; *A*, Orbit; *S*, Supratemporal fossa; *Scl*, Sclerotic plates; *Md*, Mandible; *k*, Articular; *ang*, Angular; *op*, Splenial; *d*, Dentary. (After Zittel.)

intermedius is the species least widely removed from the preceding group; while the typical *I. communis* is distinguished by the extreme width of the paddles. In a second subgroup, which ranges from the Oxford Clay to the Chalk, the roots of the teeth are invested with a thick layer of cement; the dorsal aspect of the humerus has a prominent trochanteric ridge; and the coracoid differs from that of the preceding subgroup (fig. 1026) by the absence of a posterior notch. This subgroup comprises *I. trigonus*, and probably other allied forms from the Oxford and Kimeridge Clays; and also the well-known *I. campylodon*, from the Upper Cretaceous of a large portion of Europe, to which *I. indicus*, from the corresponding strata of India, and perhaps also *I. australis*, from the Cretaceous of Australia, are probably closely allied. The former is in some respects even more specialised than the following genera. The species referred to this genus from the Polar regions are considered to be of Triassic age; and a species from Ceram may be from Cretaceous beds. The genus is unknown in America.

The most specialised representatives of the family are the genera *Opthalmosaurus*, from the Oxford and Kimeridge Clay and probably also the Cretaceous of England, and *Baptanodon* (*Sauranodon*), from the Upper Jurassic of North America. In the latter teeth, and even a dental groove, were totally wanting, but in the former small teeth were present. In the former (and probably also the

latter) the humerus (fig. 1033) and femur have a prominent trochanteric ridge, and in both they articulate distally with three distinct bones (figs. 1033-34), which in the pectoral limb are correlated

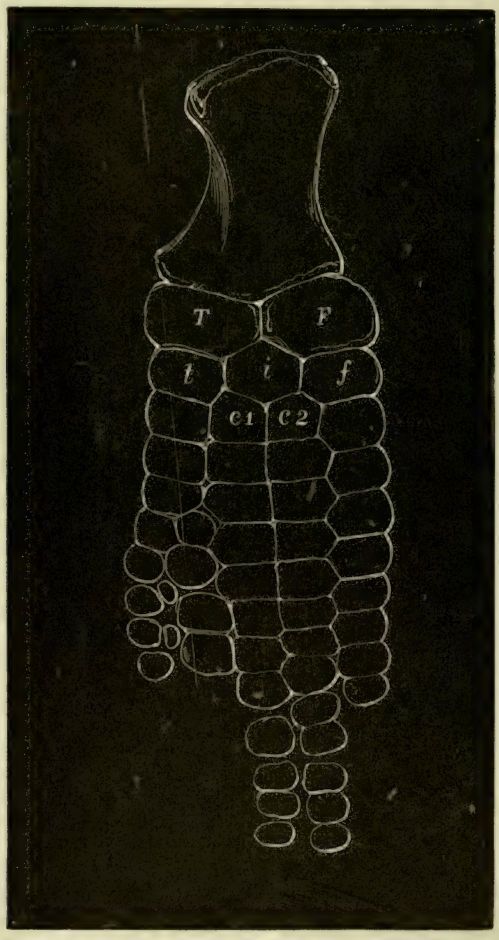

Fig. 1031.—Ventral aspect of the right pectoral limb (wanting the marginal rows) of *Ichthyosaurus intermedius*; from the Lower Lias of Gloucestershire. Reduced. *T*, Radius; *F*, Ulna; *t*, Radiale; *i*, Intermedium; *f*, Ulnare; *c1*, *c2*, Centralia. (After Hawkins and Hulke.)

by Dr Baur with the radius, ulna, and pisiform; the corresponding bones in the pelvic limb (fig. 1034) being the tibia, fibula, and the homologue of the pisiform. The clavicles differ from those of *Ichthyosaurus* in being separate. Both limbs appear to have been

of great width, and the third digit, or the one arising from the intermedium, at least in the American genus, consists of two longitudinal rows of bones. The type species of *Opthalmosaurus* was of moderate size, and occurs in the Oxford and Kimeridge Clays; it is characterised by the inequality in the size of the three distal facets of the humerus. In *O. cantabrigiensis*, of the Cambridge Greensand, which may belong to *Baptanodon*, these three facets have, however, become nearly equal in size; and this form seems therefore to indicate the highest evolution of the order. It should be mentioned that Professor Marsh and Mr Hulke differ from Dr Baur in their interpretation of the three bones of the second segment of the limb of this genus; correlating the middle bone with the intermedium, and the postaxial one with the ulna in the pectoral, and the fibula in the pelvic limb. Finally, it should be observed that a femur, from the Cambridge Greensand, described under the name of *Cetarthrosaurus*, and regarded as belonging to a member of the present order, but which has been referred by Mr Hulke to the suborder Pythono-

Fig. 1032. — Tooth of *Ichthyosaurus communis*; from the Lower Lias of Gloucestershire.

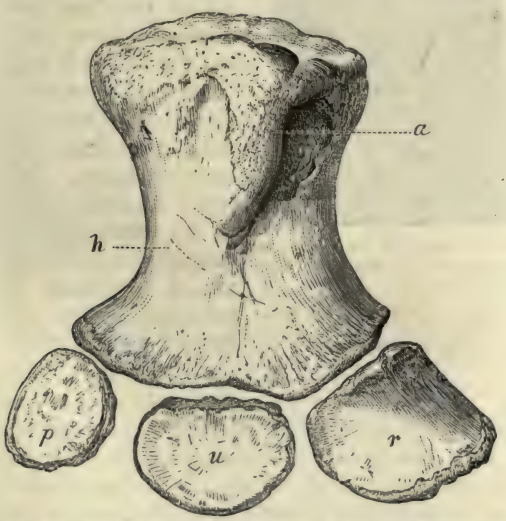

Fig. 1033.—Dorsal aspect of part of the right pectoral limb of *Opthalmosaurus icenicus*; from the Oxford Clay. One-third natural size. *h*, Humerus; *a*, Trochanteric ridge of do.; *r*, Radius; *u*, Ulna; *p*, Pisiform.

morpha of the Squamata, appears to approximate in structure to the femur of *Ichthyosaurus campylodon*, and may therefore really belong to this order.

Order V. Proterosauria.—The genus *Proterosaurus*, from the Middle Permian of Thuringia, is regarded by Professor Seeley as presenting such peculiar features that it is entitled to ordinal distinction, although Dr Baur would include it in the Rhynchocephalia. The skull is very imperfectly known, and although Professor Seeley has attempted its restoration, Professor Credner points out that the specimens scarcely justify the figure. There is some doubt as to the mode of attachment of the teeth to the jaws, but they appear to have been anchylosed to the bone, with cavities beneath them, and were not, as has been supposed, implanted in distinct alveoli. Teeth also occur on the palatine, pterygoid, and vomer; and Professor Seeley considers that the palate was closed. The dorsal vertebræ are amphicœlous, and have no intercentra; but the cervicals appear to have been opisthocœlous, and are remarkable for their length. There were intercentra in the anterior cervical region. In all the vertebræ the arches were anchylosed to the centra; while in the dorsals the costal articulation is placed unusually high. The posterior caudal vertebræ have divided neural spines. Abdominal ribs were fully developed (fig. 1035), and were apparently of the Rhynchocephalian type. It has been suggested that the ilium may have had a preacetabular production; but the pectoral girdle seems to have been of the Rhynchocephalian type, the clavicles and interclavicle, according to Dr Credner, closely resembling those of *Sphenodon*.

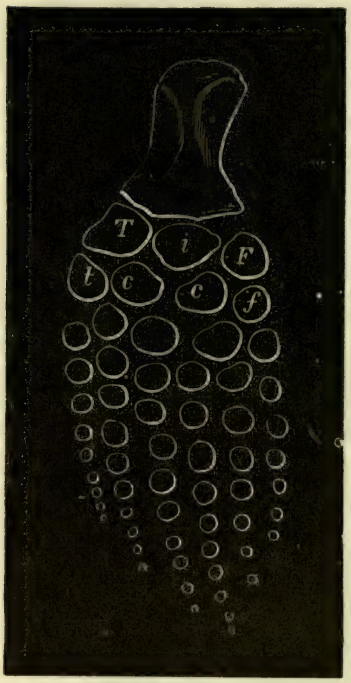

Fig. 1034.—Dorsal aspect of the left pelvic limb of *Baptanodon natans*; from the Upper Jurassic of North America. Reduced. *T*, Tibia; *i*, Fibula; *F*, Bone representing the pisiform of the manus; *t*, Tibiale; *c* (left side), Intermedium; *c* (right side), Fibulare; *f*, Undetermined bone. The two bones beneath the intermedium are the centralia. (After Marsh and Hulke.)

According to Dr Baur there are two centralia in the carpus;

while Professor Seeley describes a centrale (navicular) in the tarsus. The pectoral limb is considerably shorter than the pelvic (left side of fig. 1035); and while both have five digits, neither presents any very strongly marked divergence from the Rhynchocephalian plan of structure. In the type species there were the normal two sacral vertebræ; but according to Professor Seeley, *P. Linki* differs from all other known members of this branch in having three sacrals. It is highly probable that *Proterosaurus* should be regarded as a

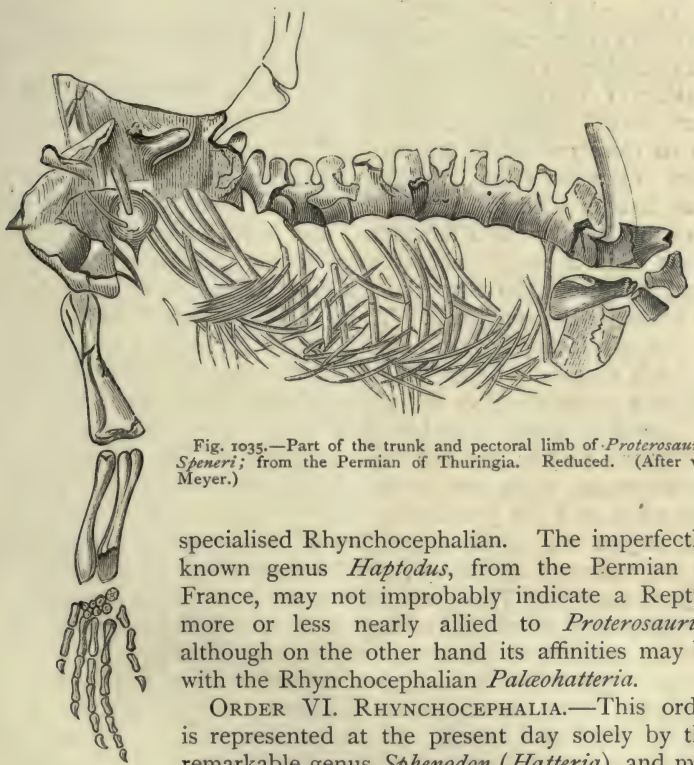

Fig. 1035.—Part of the trunk and pectoral limb of *Proterosaurus Speneri;* from the Permian of Thuringia. Reduced. (After von Meyer.)

specialised Rhynchocephalian. The imperfectly-known genus *Haptodus*, from the Permian of France, may not improbably indicate a Reptile more or less nearly allied to *Proterosaurus*, although on the other hand its affinities may be with the Rhynchocephalian *Palæohatteria.*

Order VI. Rhynchocephalia.—This order is represented at the present day solely by the remarkable genus *Sphenodon* (*Hatteria*), and may be provisionally characterised as follows: The external appearance is usually more or less lizard-like. In the skull the quadrate is immovably fixed by its proximal extremity, and unites by suture with the pterygoid; an inferior temporal arcade is present (fig. 1039); the postorbital, at least in *Sphenodon*, is quite distinct from the postfrontal; the palate is closed anteriorly by the median union of the pterygoids, which, in the living form at least, extend forwards to meet the vomers, and thus separate the

palatines;[1] and the premaxillæ never united. The dentition is usually acrodont. The ribs may have uncinate processes, and abdominal ribs are always developed. The vertebræ may be either opisthocœlous or amphicœlous, and intercentra may be retained.

Dr Baur observes that "the Rhynchocephalia, together with the Proterosauria, to which they are closely allied, are certainly the most generalised group of all Reptiles, and come nearest, in many respects, to that order of Reptiles from which all others took their origin."

This order, if we include *Palæohatteria*, dates from the Permian, but only comparatively few forms are at present known. It may be provisionally divided into three suborders.

Family Palæohatteriidæ.—The genus *Palæohatteria*, of the Permian of Germany, is regarded by Professor Credner, its describer, as so closely allied to the existing *Sphenodon* that it is referred by him to the same family. There can, however, be no question but that it is entitled to be the representative of a distinct family, and probably of a distinct suborder. Dr Baur, with whom Professor Cope is in accord, would even go farther, and remove this genus altogether from the Rhynchocephalia, to place it with *Mesosaurus* in his order Proganosauria. There is, indeed, much to be said in favour of placing both these primitive Reptiles in a single group; but this appears to be outweighed by the resemblance of the one to the true Sauropterygians and of the other to the Rhynchocephalians.

The skull much resembles that of *Sphenodon*, the jugal dividing posteriorly to join the two temporal arcades; but the supra- and infratemporal fossæ are much smaller, while there is a separate lachrymal, and the premaxillæ do not form a beak. Teeth occur not only on the palatines, but also on the vomer and pterygoids, as in the young of *Sphenodon;* and Dr Baur suggests that there was a parasphenoid. There are intercentra between all the vertebræ, in which the neural arches remain distinct from the centra; there are also two sacral vertebræ; and the ribs have no uncinate processes. The teeth of the jaws were acrodont, and anchylosed to the bone. The pectoral girdle presents an approximation, in the form of the clavicles and interclavicle, to that of *Sphenodon;* but the expanded proximal extremities of the clavicles recall the lateral thoracic plates of the Labyrinthodonts, and the coracoid is more like that of the Sauropterygians. This bone, indeed, like the bones of the pelvic girdle, ossifies by radiations from the centre after the manner obtaining in Sauropterygians and Amphibians. The pelvic girdle is widely different from that of *Sphenodon;* the pubes and ischia forming wide flattened plates like those of the Sauropterygian

[1] The same arrangement obtains in the skull of *Nothosaurus*, represented in fig. 991.

genus *Mesosaurus*, and the ischia being almost identical with those of the Amphibia. The tarsus also resembles that of *Mesosaurus* in having five distinct bones in the distal row; while the humerus (as in the latter) has an entepicondylar, or ulnar, foramen.

That *Palæohatteria* is a primitive type connecting the later Rhynchocephalia with the Amphibia there can be no reasonable doubt; and although it presents many points of affinity with *Mesosaurus*, these resemblances are those which we should expect to find in all transitional types, and do not necessarily imply that all the forms in which they occur should be placed in the same group.

Suborder 1. Simædosauria.—This group is represented by the genus *Champsosaurus*, typically from the Lower Eocene of North America, which may be regarded as a somewhat specialised Rhynchocephalian, showing a remarkable affinity, in the general structure of its skull and vertebral column, to *Hyperodapedon*. Dr Baur observes that this genus agrees with the other Rhynchocephalia in the loose condition of the otic bones, and in the nature of the costal articulations; and since it has a fixed quadrate, two temporal arcades, and abdominal ribs, there appears no good reason for its ordinal separation. The adaptation to an aquatic life has, however, necessarily produced considerable structural modifications of secondary import. The correctness of these observations has been remarkably shown by the researches of M. Dollo, who finds that the structure of the palate, and the position of the posterior nares, and the general arrangement of the teeth, closely accords with that obtaining in *Hyperodapedon*. The suborder may be characterised as follows: The facial portion of the skull is produced into a long rostrum; the splenial bone enters into the mandibular symphysis; the tail and pelvic limbs are elongated; the vertebræ are amphicœlous; and the ribs have no uncinate processes.

Family Champsosauridæ.—In the type and only known family the nares are single and subterminal; the maxillary and anterior mandibular teeth are large and not fixed to the bone; there is a series of smaller teeth on the palatines and vomers, separated by a groove from those of the maxilla; while there is also an irregular mass of small teeth on the pterygoids, which are completely united in the middle line; the posterior nares form very narrow slits on the sides of the palate; and there is no parietal foramen. There are some twenty-five presacral vertebræ, and the neuro-central suture is persistent. Remains referred to *Champsosaurus* have been found not only in the Lower Eocene of North America, but also in the corresponding horizon of Belgium and Rheims; the latter specimens having been described under the name of *Simædosaurus*. One of the specimens from Rheims indicates an animal of about nine feet in length, but other examples appear to have been of considerably

larger dimensions. The Simædosauria may perhaps be regarded as an offshoot from a stock related to *Hyperodapedon*.

Suborder 2. Sphenodontina.—This group is characterised by the short and more or less triangular skull, in which the premaxillæ are produced into a distinct beak; by the longitudinal series of palatine teeth, separated by a groove (into which the hinder mandibular teeth are received) from those of the maxilla (fig. 1037); and by the presence of uncinate processes to the ribs.

Family Rhynchosauridæ.—This is the most specialised family, and as being most nearly related to *Champsosaurus*, may be noticed first. The nares are single; there are no teeth either in the beak or in the opposing part of the mandible, which were probably cased in horn; there may be more than a single row of palatine teeth; and the presacral vertebræ may be more or less opisthocœlous.

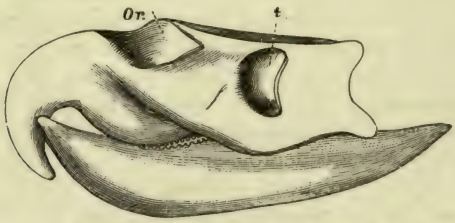

Fig. 1036.—Left lateral view of the skull of *Hyperodapedon Gordoni*, as restored by Professor Huxley; from the Trias of Elgin. Reduced. *Or*, Orbit; *t*, Infratemporal fossa.

The most specialised genus *Hyperodapedon* was originally made known to us by some very imperfect specimens from the Keuper or Upper Trias of Elgin and Warwickshire; but the subsequent discovery of a nearly entire skeleton in the former locality has enabled Professor Huxley to illustrate its full affinities. Remains referred to the same genus also occur in the Maleri stage of the Gondwana system of Central India. The European species attained a length of from six to seven feet, but the Indian form must have been nearly or quite double these dimensions. The skull (fig. 1036) is remarkable for its depressed and triangular form, in which it resembles that of the Chelonian family *Chelydridæ;* and also for the upward direction of the small orbits; the reduced size of the infratemporal fossæ; the strongly-curved and thick premaxillary beak; the diverging clawlike processes of the mandibular symphysis; and the absence of a parietal foramen. Professor Huxley considered that the forked extremities of the mandibular symphysis embraced the premaxillary beak, as is shown in the figure; but later observations indicate that they were received in a pit beneath the beak, which Professor Huxley regarded as containing the apertures of the posterior

nares. The latter probably really formed very small slits on the sides of the palate, as in *Champsosaurus*, and opened between the rows of maxillary and palatine teeth. By far the most remarkable feature is, however, to be found in the upper dentition. On the palatal surface of the peculiar triangular compound bone (fig. 1037), which may be conveniently termed the palato-maxilla, although anteriorly it probably includes the vomer, and posteriorly part of the pterygoid, there are, on the outer or maxillary side, several rows of low pyramidal teeth; then comes the groove for the reception of the edge of the mandible, on the inner side of which there are two or more rows of similar teeth borne by the palatine and vomer, and probably also by the pterygoid. And it is interesting to notice that while in the type species the larger number of rows of teeth occurs on the palatine and vomer, the reverse condition obtains in the Indian form (fig. 1037). In the type species there appears to be no foramen to the humerus, and the presacral vertebræ are slightly opisthocœlous; it is, however, not improbable that the vertebræ of the Indian form were amphicœlous. The extremely solid structure of the palato-maxilla causes this part to be the most frequently preserved; and these bones are very common in the Indian Gondwanas.

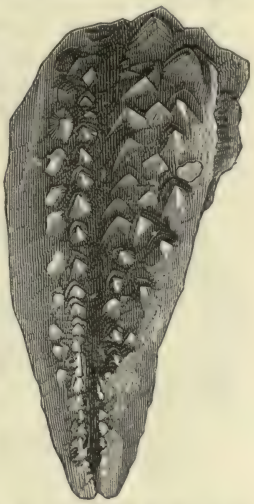

Fig. 1037.—Oral surface of the right palato-maxilla of *Hyperodapedon Huxleyi*; from the Maleri stage of Central India. (After Medlicott and Blanford.)

Professor Huxley observes that it is very interesting to note that this suborder had attained its greatest degree of specialisation as early as the Trias; *Hyperodapedon* being in all respects a more modified form than *Sphenodon*. It appears therefore to be probable that in the Permian, or perhaps still earlier, there must have existed Lizards differing less from the existing genus than either *Hyperodapedon* or *Rhynchosaurus*.

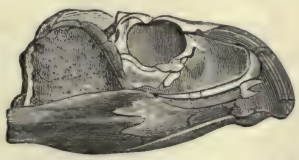

Fig. 1038.—Right lateral aspect of the skull of *Rhynchosaurus articeps*; from the Trias of Warwickshire. Reduced. (After Owen.)

In the typical genus *Rhynchosaurus*, from the English Keuper, of which the type skull is represented in fig. 1038, there is but a single row of palatine teeth; the orbit is large and lateral; the infratemporal fossa of considerable size; and the premaxillary beak long and slender, its form being not

correctly shown in the figure of the type skull. The single described species indicates an animal about three feet in length. This genus serves in some respects to connect *Hyperodapedon* with *Sphenodon*.

Family Sphenodontidæ.—The least specialised family of this suborder is solely known by the existing New Zealand genus *Sphenodon* (*Hatteria*), of which the cranium is shown in fig. 1039. According to Professor Huxley's definition, this genus is characterised by the divided nares; the presence of a single tooth on either side of the premaxillary beak, which was not sheathed in horn; by the single row of palatine teeth; and the amphicœlous vertebræ. In the palate the pterygoids unite anteriorly with the vomer to exclude the palatines from the median line. Additional distinctive features are found in the presence of intercentra between all the vertebræ; in the large size and the lateral position of the orbits; the well-developed parietal foramen; and the large size of the supra- and infratemporal fossæ (fig. 1039). The humerus is remarkable as having both an entepicondylar and an ectepicondylar foramen.

Fig. 1039.—Right lateral view of the cranium of *Sphenodon punctatus*, of New Zealand. (After Günther.)

The Tuataras, as these lizards are called by the Maories, are medium-sized reptiles of extreme rarity, and with nocturnal habits. The alveolar border of the dentary bone of the mandible is received in the groove between the palatine and maxillary teeth, and in old individuals becomes as hard and polished as the teeth themselves, of which it eventually discharges the functions.

Suborder 3. Homæosauria.—This group includes several genera of Mesozoic Reptiles, in which the premaxillæ did not apparently form a beak, and the ribs were devoid of uncinate processes. The dentition is acrodont; but the nature of the palatal dentition is unknown. The vertebræ are amphicœlous, and Dr Baur considers that intercentra were present.

Family Homæosauridæ.—The type family is definitely known from the Kimeridgian Lithographic slates of the Continent, and is characterised as follows. The body is shaped like that of ordinary Lizards; the skull is comparatively broad and short, with oval nares, and a complete postorbital bar; there are no tusk-like teeth in the premaxillæ or mandible; and the pes is of normal structure. The

Kimeridgian genera are *Homœosaurus*, *Ardeosaurus*, and *Sapheosaurus*; all of which are represented by species of small or medium size. The imperfectly known *Aphelosaurus*, from the Permian of France, was regarded by the late Professor Gervais as allied, but it may indicate a distinct family, which does not belong to this group; the number of phalangeals is the same as in existing Lizards.

Family Pleurosauridæ.—This family is typically represented by *Pleurosaurus*, of the Kimeridgian of Bavaria, which is a medium-sized Lizard characterised by the extreme elongation of the body (in which there are a great number of presacral vertebræ), and the long narrow skull, with slit-like nares. *Anguisaurus* and *Acrosaurus*, of the same deposits, belong to this family; but it does not appear certain that they are really distinct from the type genus.

Family Telerpetidæ. — The small *Telerpeton*, of the Upper Trias of Elgin, differs from the *Homœosauridæ* by the presence of tusk-like teeth at the extremities of both jaws, and the reduction in the number of the phalangeals of the fifth digit of the pes to two; in addition to which Professor Huxley considers that the skull had no postorbital bar. The one species is of small size; and although the genus agrees with the *Homœosauridæ* in its acrodont dentition, its serial position must be regarded as provisional. *Saurosternum*, from the Karoo system of South Africa, is not improbably an allied genus; although it has been referred by Sir R. Owen to the Amphibian Labyrinthodonts under the name of *Batrachosaurus*.

Finally, it should be mentioned that Professor Cope includes in the present order the genera *Typothorax* and *Aëtosaurus*, which are here provisionally placed, on the authority of Dr Baur, among the Crocodilia.

Order VII. Squamata.—With this order we come to the consideration of the one represented most numerously at the present day, and containing the true Lizards, the Chamæleons, the extinct Mosasaurians, and the Serpents. In this order the body may be either short, with well-developed limbs and distinct tail (lacertiform); or it may be extremely elongated, without any external trace of limbs, and passing gradually into the tail. As a rule, the whole body and limbs are covered with overlapping horny scales; and these may be underlain by an armour of bony dermal scutes. The limbs may be adapted either for walking on land, or modified into paddles for swimming. In the skull the proximal end of the quadrate is more or less movably articulated; the lower temporal arcade is wanting; the postorbital is generally fused with the postfrontal; the palate is more or less open, the pterygoids being nearly always separated by an interval from one another; and the premaxillæ are

frequently united. The vertebræ are generally procœlous, although rarely amphicœlous; their neurocentral suture is always obliterated; zygosphenal articulations may or may not be present; and intercentra are always wanting. The dorsal ribs never have uncinate processes; and true abdominal ribs are likewise never developed. The carpus has but a single centrale; and the precoracoidal process (fig. 1040) is often well marked.

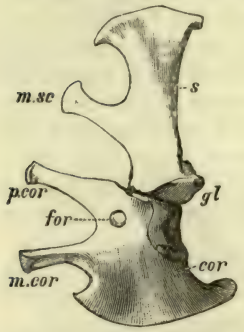

Fig. 1040.—Part of the left pectoral girdle of *Iguana*. *s*, Scapula; *m.sc*, Mesoscapula; *cor*, Coracoid; *p.cor*, Precoracoid; *m.cor*, Mesocoracoid; *for*, Foramen; *gl*, Glenoid cavity.

Three of the groups here regarded as suborders of the Squamata are frequently ranked as distinct orders, but their mutual relations are so close that it appears to harmonise better with the classification, adopted in other branches of the class, to include the whole of them in a single order. The Squamata may be regarded as occupying a position among Reptiles somewhat similar to that held by the Teleostei among Fishes, and the Passeres among Birds. That is to say, they are essentially typical Reptiles, which have attained to a considerable degree of specialisation; and while they have lost, on the one hand, all signs of kinship with the Amphibians, they exhibit, on the other, no traces of especial relationship with the Birds. That this order has originated from the Rhynchocephalia there seems but little doubt; but we are very much in the dark as to when or how the divergence took place.

Suborder 1. Lacertilia.—In the true Lizards the four limbs are usually well developed (fig. 1041) but in some cases one or both pairs are wanting. The ali- and orbitosphenoidal regions of the skull are imperfectly ossified; the superior temporal arcade is generally present; the quadrate articulates with the pterygoid; the nasals form a part of the narial aperture; and the rami of the mandible unite by suture. The vertebræ are in some instances amphicœlous; they usually have no zygosphenes, and the number in the cervical region does not exceed nine. When limbs are present the pectoral girdle is complete; and the terminal phalangeals of the feet are clawed. Dermal scutes are sometimes present; and these may be developed on the upper surface of the skull, so as to roof over the supratemporal fossæ. Existing Lizards are divided into twenty families, but only those will be noticed which occur in the fossil state.

We may commence our notice with a few Mesozoic forms, of which the family position is not yet determined. The earliest

known form appears to be *Macellodus* (with which *Saurillus* is either identical or very closely allied), from the English Purbeck; a small Lizard with pleurodont dentition, dermal scutes, and procœlous vertebræ. *Adriosaurus* is a larger form from the Lower Greensand of Austria, also having dermal scutes and procœlous vertebræ, but of which the dentition is unknown. An allied Continental Mesozoic form has received the name of *Hydrosaurus*, which is, however, a synonym of *Varanus*. In the Cambridge Greensand an imperfect femur and a vertebra indicate a Lizard of the size of some of the existing Monitors, but of which the affinity cannot even

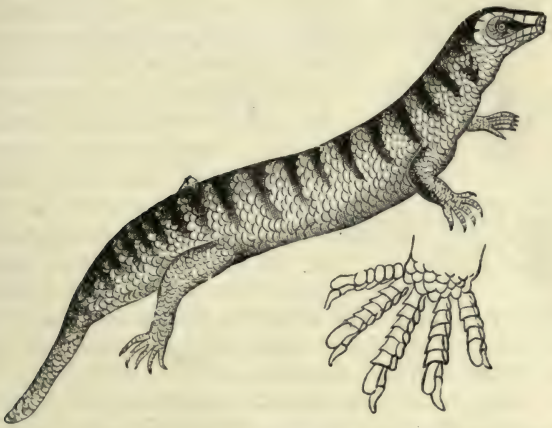

Fig. 1041.—The common Skink (*Scincus officinalis*). Reduced.

be conjectured. In the English Chalk occur the imperfectly known genera *Coniasaurus* and *Raphiosaurus;* the former having expanded, and the latter acute teeth.

Here also may be mentioned several genera from the Tertiaries of North America, of which the family position cannot yet be determined. The Eocene forms have been named *Tinosaurus* and *Thinosaurus*, and those from the Miocene *Aciprion*, *Platyrhachis*, and *Cremastosaurus*. *Notosaurus*, from the Tertiary of Brazil, has amphicœlous vertebræ, and may be a Rhynchocephalian.

Family Agamidæ.—The Agamoid Lizards constitute a large family, mainly characteristic of Asia, but also occurring in Europe, Africa, Australia, and Polynesia. The supratemporal fossa is not roofed over; the dentition is acrodont; and the premaxillæ are separate. Specimens referred to the type genus *Agama* have been obtained from the Upper Eocene Phosphorites of Central France; while the Pleistocene of Australia has yielded a skull indistinguish-

able from that of the existing Frilled Lizard (*Chlamydosaurus Kingi*) of the same country.

Family Iguanidæ.—The Iguanoids are readily distinguished from the *Agamidæ* by their pleurodont dentition (fig. 1042), and the presence of zygosphenal articulations to their vertebræ (fig. 1043). Nearly all the genera are now confined to the New World. In the Upper Eocene (Oligocene) Phosphorites of Central France there occur, however, fragments of jaws which have been referred to the typical American genus *Iguana;* that term being used in a wider sense than in recent herpetology. Vertebræ also occur in the approximately equivalent deposits of Hordwell in Hampshire (of which one is represented in fig. 1043), which agree in the presence of small zygosphenes with those of existing Iguanas, and have been provisionally referred to the French species. The name *Iguanavus* has been applied to remains of a member of this family from the Eocene of North America.

Fig. 1042.—Inner view of left ramus of the mandible of *Iguana*.

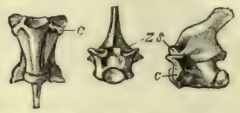

Fig. 1043.—Vertebra of *Iguana europæa*, viewed from the hæmal, anterior, and lateral aspects; from the Upper Eocene of Hampshire. *zs*, Zygosphene; *c*, Costal tubercle.

Family Anguidæ.—The *Anguidæ* are characterised by the presence of scutes roofing over the supratemporal fossæ; by the separation of the premaxillæ and the nasals; the more or less completely pleurodont dentition; and the presence of dermal scutes covered with minute tubercles. The genus *Ophisaurus* (*Pseudopus*), in which the limbs are either wanting or are reduced to rudiments of the pelvic pair, is represented in the Middle Miocene of Gers, in France, and the Lower Miocene of Rott, near Bonn; some of the species having been originally described under the name of *Anguis*. *Propseudopus*, from the Middle Miocene of Steinheim, in Bavaria, is distinguished from *Ophisaurus* by its stronger dentition and the presence of a double row of teeth on the vomer. The genus *Peltosaurus* and the allied *Exostinus*, of the Miocene of North America, may be included in this family; to which we may also refer several European and American Upper Eocene genera which have been regarded as constituting a distinct family under the names of *Placosauridæ* and *Glyptosauridæ*. Among these *Placosaurus* (*Palæovaranus*), from the Upper Eocene of France and England, has teeth resembling those of the Slow-worm (*Anguis*), which were originally regarded as belonging to a Varanoid; the vertebræ (fig. 1044) are not unlike

those of the existing *Diploglossus*, and the limbs were well developed. Another Anguoid, with blunt cylindrical teeth, from the Quercy Phosphorites, was originally referred to the Scincoid genus *Eumeces* (*Plestiodon*), but its generic position must for the present remain undecided. In North America we have *Glyptosaurus*, from the Bridger Eocene of Wyoming, in which the vertebræ have rudimental zygosphenes; the large *Saniva*, of which the dermal scutes are unknown; and the apparently allied *Xestops* (*Oreosaurus*). The vertebræ of these genera, like those of existing *Anguidæ*, present a strong resemblance to those of the next family, as may be seen by comparing fig. 1044 with fig. 1045.

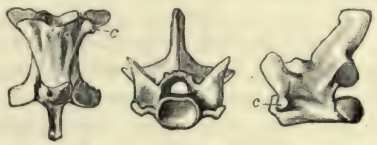

Fig. 1044.—Vertebra of *Placosaurus margariticeps*, viewed from the hæmal, anterior, and lateral aspects; from the Upper Eocene Phosphorites of Central France. *c*, Costal tubercle.

Family Varanidæ.—The Monitors include the largest known Lizards; one of the fossil species attaining a gigantic size. They are confined to the Old World and Australia; and appear to be unknown before the Pliocene. The skull has no postorbital bar; the supratemporal fossæ are not roofed over by bony scutes; and both the premaxillæ and the nasals are united. The dentition is pleurodont; and the teeth are large and pointed, and confined to the jaws. The vertebræ are characterised by their broad and flat centra (fig. 1045); and dermal scutes are wanting. All the known forms may be included in the single genus *Varanus*.

In existing forms the dorsal vertebræ are elongated, and have broad neural spines; and the largest species attains a length of seven feet. In a fossil state this group is represented by remains from the Pleistocene of Madras apparently referable to the living *V. bengalensis*. Other vertebræ, again, found in the corresponding cave-deposits of Queensland, not improbably belong to one or more of the species still inhabiting that region. In a second and extinct group the dorsal vertebræ are relatively shorter and wider, and have narrower neural spines; the two known species being of very large size. The smaller of the two is *V. sivalensis*, from the Pliocene of the Siwalik Hills of India, of which a dorsal vertebra is shown in fig. 1045. Another vertebra is, however, larger than the figured specimen; and the total length of the animal was probably at least twelve feet. These dimensions were, however, greatly exceeded by the huge *V. priscus*, of the Pleistocene of Australia, in which

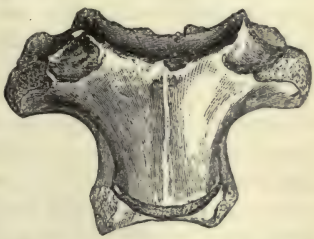

Fig. 1045.—Hæmal aspect of a dorsal vertebra of *Varanus sivalensis*; from the Pliocene of the Siwalik Hills.

the vertebræ are three times the size of those of *V. sivalensis*, and the total length did not probably fall short of thirty feet. This species was originally described by Sir R. Owen under the name of *Megalania;* certain remains which were referred to it having subsequently proved to be Chelonian. An imperfectly known species, from the Lower Pliocene of Attica, may perhaps belong to the former group.

It may be well to mention here that Sir R. Owen has described two peculiar, blunt and pleurodont teeth of a large lizard from the Pleistocene of Queensland under the name of *Notiosaurus*, which is, however, preoccupied by the genus *Notosaurus* (p. 1139). It is just possible that these teeth may be referable to *Varanus priscus*, in which event the generic term *Megalania* would have to be retained for that form.

Family Teiidæ.—In this family, which is confined to America, the supratemporal fossæ of the skull are not roofed over, the dentition is pleurodont or subacrodont; the teeth, although variable in form, are always solid at the base; and there are no dermal scutes. An existing species of *Tupinambis* is represented in the Pleistocene cave-deposits of Brazil.

Family Lacertidæ.—In the *Lacertidæ* the supratemporal fossæ are roofed over by bone; the premaxillæ are united; the dentition is pleurodont, the bases of the teeth being hollow; and there are no dermal scutes. All the genera belong to the Old World. Remains of the existing *Lacerta ocellata* occur in the Pleistocene of France, and extinct species referred to the same genus have been described from the Miocene and the Upper Eocene Phosphorites of the same country.

Family Scincidæ.—The Scincoid Lizards form a large cosmopolitan family, characterised by the bony scutes roofing over the supratemporal fossæ; the separate or imperfectly united premaxillæ; the pleurodont dentition; and the presence of dermal scutes. *Dracænosaurus*, of the Lower Miocene of France, is an extinct genus with molariform teeth, probably allied to the existing *Scincus* (fig. 1041) or *Chalcides*.

Suborder 2. Rhiptoglossa.—The *Chameleontidæ*, or Chameleons, differ from the Lacertilia in that the nasals do not enter into the borders of the nares; the pterygoid does not articulate with the quadrate; and, although limbs are present, there are no clavicles or interclavicle. The dentition is acrodont. All the existing forms are Old World; but Dr Leidy has described part of a mandible from the Upper (Bridger) Eocene of Wyoming, which he refers to the type genus *Chameleon*.

Suborder 3. Dolichosauria.—This group was originally formed for the reception of the genus *Dolichosaurus*, from the English Chalk; which is a small snake-like Lizard, with more than nine

vertebræ in the neck, and well-developed limbs. The vertebræ have zygosphenal articulations. *Acteosaurus*, from the Cretaceous of Austria, is an allied form.

Suborder 4. Pythonomorpha.—The Mosasauroids are carnivorous marine Reptiles, frequently of large dimensions, and ranging in time from the Upper Greensand to the topmost Cretaceous, with a cosmopolitan distribution. The body is much elongated. The skull (fig. 1047) presents a strong resemblance to that of the *Varanidæ* among the Lacertilia, and has the nasals and premaxillæ welded together, the quadrates very loosely articulated, teeth on the pterygoids as well as in the jaws, and frequently ossifications in the sclerotic of the eye. The teeth are large and sharp, and anchylosed by expanded bases to the summits of the jaws. There may be zygosphenal articulations to the vertebræ, and the cervical region may include more than nine vertebræ. The clavicles are always, and the interclavicle and sacrum generally, wanting; but Professor Marsh figures a sternum in one genus. The limbs are modified into paddles (fig. 1046), with no claws to the terminal phalangeals, and no foramen to the humerus. The development of the pelvis is, moreover, but imperfect, and at least the majority of forms appear to have been devoid of dermal scutes, although Professor Marsh has recorded their presence in one genus.

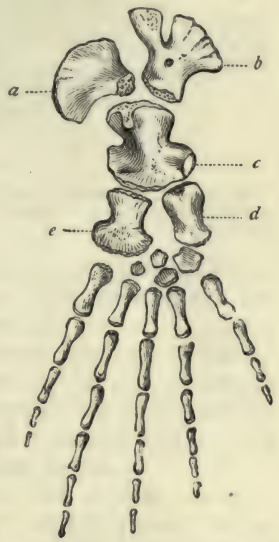

Fig. 1046.—Right pectoral limb of *Platycarpus*; from the Cretaceous of North America. One-twelfth natural size. *a*, Scapula; *b*, Coracoid; *c*, Humerus; *d*, Radius; *e*, Ulna. (After Marsh.)

Family Plioplatycarpidæ. — The least specialised form seems to be the genus *Plioplatycarpus*, of the Upper Cretaceous of Holland, in which both an interclavicle and a sacrum are present; on which account its describer, M. Dollo, regards it as the type of a distinct family.

Family Mosasauridæ.—The whole of the remaining genera of the suborder may be included in this family. One of the well-known genera is *Clidastes* (from which *Edestosaurus* is regarded by Professor Cope as inseparable), from the Cretaceous of North America. This genus comprises numerous species, characterised by the extreme elongation of the body, and their small or medium size. In the skull the teeth, as in the next genus (fig. 1047) are continued to the extremity of the premaxillæ; the vertebræ are

long, and have zygosphenal articulations; the humerus is short; and the chevrons are anchylosed to the centra. *Sironectes* is an allied genus from the same deposits, in which the chevrons are not anchylosed to the vertebræ. *Platycarpus*[1] (*Lestosaurus*, *Taniwhasaurus*), which is found in the Cretaceous of North America, New Zealand, and perhaps Europe, differs from both the preceding

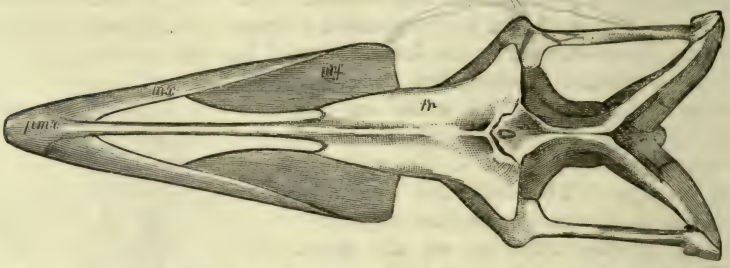

Fig. 1047.—Frontal aspect of the cranium of *Platycarpus curtirostris*; from the Upper Cretaceous of North America. Greatly reduced. *pmx*, Premaxilla; *mx*, Maxilla; *fr*, Frontal; *prf*, Prefrontal. (After Cope.)

genera by the absence of zygosphenes; the chevrons being free and the humerus (fig. 1046) short and broad. With the genus *Liodon*, in which Professor Cope includes *Tylosaurus* (*Rhinosaurus*) of Professor Marsh, we come upon forms attaining gigantic dimensions, in which the body is proportionately shorter than in the above-mentioned genera, and the vertebræ are always without zygosphenes. In *Liodon* itself the extremity of the premaxillæ is devoid of teeth, and forms a cylindrical rostrum; the teeth are smooth and more or less laterally compressed; the humerus is long; and the chevrons are free. It occurs in the Cretaceous of Europe, North America, and New Zealand. *Hainosaurus*, again, of the Upper Chalk of Mons, agrees with *Liodon* in its edentulous rostrum and free chevrons, but has teeth of three types. Some of the teeth are subcylindrical, and others compressed, with serrated cutting edges like those of *Megalosaurus*. The total length of this huge Reptile is estimated at about 40 feet. The typical genus *Mosasaurus* is definitely known from the topmost Cretaceous of Maastricht in Holland, and the Cretaceous of North America; the type species from Maastricht having been made known to science in the last century. It is characterised by the premaxillæ being toothed to their extremity; by the teeth having their crowns faceted and more or less compressed; as well as by the greater number of the chevrons being anchylosed to the vertebræ. The fine skull of *M. Camperi* represented in the accompanying woodcut was obtained from Maastricht previously to 1785, and is preserved

[1] Amended from *Platecarpus*.

in the Paris Museum. This species is estimated to have attained a length of 25 feet. Closely allied to *Mosasaurus* is *Pterycollasaurus*, which is, however, readily distinguished by the complete union of the pterygoids in the middle line—a feature unknown elsewhere

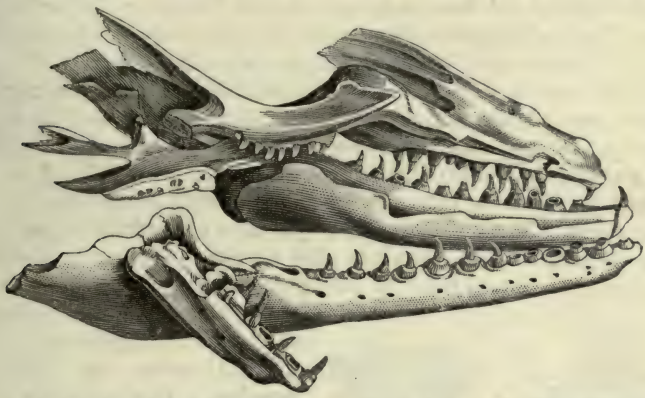

Fig. 1048.—The imperfect skull of *Mosasaurus Camperi;* from the Upper Cretaceous of Maastricht. Much reduced. The displaced bone in the left bottom corner is the left pterygoid, the corresponding bone of the opposite side being in its natural position above.

in the whole order. The only known species is *P. Maximiliani*, of the Cretaceous of Brazil. Finally, the genus *Baptosaurus*, of the Cretaceous of North America, is distinguished from all other genera by the complete union of the hæmal spines of the cervical vertebræ

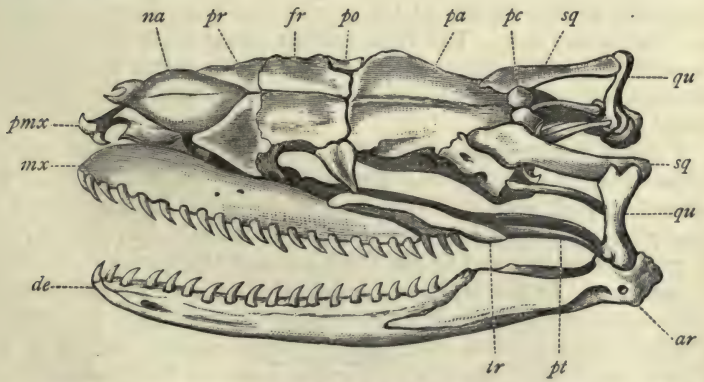

Fig. 1049.—Left lateral and upper view of the skull of *Boa*. *pmx*, Premaxilla; *na*, Nasal; *pr*, Prefrontal; *fr*, Frontal; *po*, Postfrontal; *pa*, Parietal; *pc*, Proötic; *sq*, Squamosal; *qu*, Quadrate; *pt*, Pterygoid; *tr*, Transverse; *mx*, Maxilla; *ar*, Articular; *de*, Dentary.

with the centra. The Mosasaurs attained their maximum development at a time when the Ichthyosaurs were on their decline.

The very imperfectly known *Cetarthrosaurus*, of the Cambridge Greensand, which Mr Hulke refers to this order, is noticed among the Ichthyopterygia.

Suborder 5. Ophidia.—The Serpents and Snakes constituting the last division of the Squamata present the following distinctive features: The body is greatly elongated (fig. 1051, *bis*), and the vertebral column divisible only into a trunk and a caudal region. The alisphenoidal region of the skull is fully ossified; there is no temporal arcade, parietal foramen, or columella; the quadrate and the bones of the palatal and maxillary regions are loosely attached to the skull (fig. 1049); the premaxillæ are more or less aborted and usually edentulous; and the two rami of the mandible are connected only by ligament. The vertebræ (fig. 1050) have zygosphenes; but there is no sacrum, and chevrons are also wanting. There is, moreover, no sternum, nor any trace of the pectoral girdle or limbs; but in some cases there are rudiments of the pelvic girdle and limbs. Dermal scutes are invariably wanting. This suborder is divided into three sections; but since its palæontological history is but imperfectly known, only very brief mention will be made of those families represented in a fossil state. With the exception of an imperfectly known form from the Chalk, described under the name of *Cimoliophis*, all the known fossil forms are of Tertiary or Post-tertiary age. The next earliest genus is *Helagrus*, of the Lowest (Puerco) Eocene of North America, in which the imperfect development of the zygantrum of the vertebræ indicates very generalised affinities.

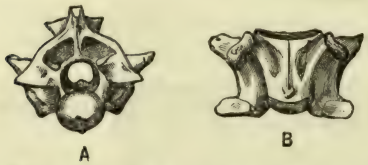

Fig. 1050.—Posterior (A) and hæmal (B) views of a trunk vertebra of *Python molurus*; from the Pleistocene of India.

Family Colubridæ.—The first existing family of the section Colubriformes, or Innocuous Snakes, contains the great bulk of the suborder; and, with the exception of Australia, is represented in nearly all temperate and warm regions. The Indian genus *Ptyas* is probably represented in the Pleistocene of Madras by the existing *P. mucosus*. In the Middle Miocene of France we have the extinct *Pilemophis* closely related to the modern *Tropidonotus*, or common English Snake; while the existing genus *Elaphis* occurs in the Upper and Lower Miocene of various parts of the Continent. A species of *Periops* closely allied to one now living in Egypt occurs in the Pleistocene of Coudes, in the south of France; and *Thamnophis*, from the Middle Miocene of the latter country, is said to be allied to *Elaphis*.

Family Pythonidæ.—The Pythons, or Rock Snakes, are now

confined to Africa, Asia, or Australia; and, with the next family, include the largest existing representatives of the suborder. They have teeth in the premaxilla; and all of them are good swimmers. Remains of the existing Indian *Python molurus* (fig. 1050) are found in the Pleistocene of Madras; and not improbably also in the Pliocene of the Punjab; while in the Pleistocene of Australia occur vertebræ probably referable either to *Narboa* or *Liasis*, which now inhabit that continent. From the Upper Eocene (Lower Oligocene) freshwater deposits of Hampshire, and the equivalent Phosphorites of Central France, we have the genus *Paleryx* (*Palæopython*), which is apparently nearly related to *Python*. Finally, *Scytalophis*, from the Quercy Phosphorites, is said to connect the *Pythonidæ* with the *Tortricidæ*.

Family Boidæ.—The Boas are at the present day confined to the New World, and differ from the *Pythonidæ* by the absence of premaxillary teeth (fig. 1049). The genera *Boavus*, *Lithophis*, and *Lestophis* (*Limnophis*), of the Upper Eocene of North America, are probably referable to this family. *Protagrus*, from the same deposits, may also be provisionally included in this family; to which it has been suggested that *Botrophis*, of the French Miocene, may likewise belong.

Family Erycidæ.—The members of this family are small Snakes allied to the *Boidæ*, but having a much shorter and non-prehensile tail. *Scaptophis*, of the Middle Miocene of France, is regarded as allied to the existing African *Eryx*; while in the Miocene of North America we have *Aphelophis*, *Calamagrus*, and *Ogmophis*, all of which appear to be more or less closely related to the genus *Charina* now inhabiting the same regions.

Family Palæophidæ.—Here we may provisionally place the family formed for the reception of the extinct genus *Palæophis*,

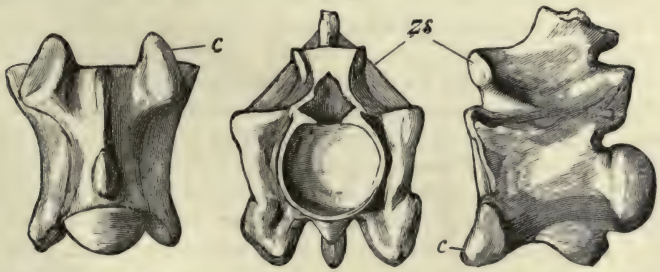

Fig. 1051.—Vertebra of *Palæophis typhæus*; from the Middle Eocene of England. The neural spine is wanting. *c*, Costal tubercle; *zs*, Zygosphene.

from the Lower and Middle Eocene of Europe, comprising very large Serpents, which were probably of marine habits. The ver-

tebræ (fig. 1051) differ from those of the *Pythonidæ* (fig. 1050) by their much taller neural spines, the lower position of the costal articular surfaces, the less divergence of the zygapophyses, and by the stronger development of the hæmal ridge on the inferior aspect of the centrum, which often carries well-marked processes at its two extremities. The type genus *Palæophis* is represented by three English species, of which the largest is estimated to have attained a length of 20 feet. In the Eocene of North America we have closely allied forms reaching to a length of 30 feet, which are referred by Professor Marsh to a distinct genus under the name of *Titanophis* (*Dinophis*), but which Professor Cope regards as indistinguishable from *Palæophis*. By Sir R. Owen these snakes are regarded as allied to the existing marine Sea-snakes or *Hydrophidæ*.

Family Elapidæ. — The first existing family of the section Colubriformes Venenosi includes the Cobras (*Naia*, fig. 1051, *bis*) and Coral-snakes (*Elaps*). The former genus probably occurs in the Pleistocene of Madras; and perhaps also in the Middle Miocene of Steinheim, in Bavaria.

Family Viperidæ.—The present and following families constitute the section Viperiformes; characterised, among other features, by the perfect development of the poison-apparatus. A snake from the Upper Miocene of Switzerland has been referred by M. Rochebrune to the existing genus *Bitis* (*Echidna*); having been originally described under the name of *Coluber Kargi*.

Family Crotalidæ.—The Pit-Vipers and Rattlesnakes are confined at the present day to Asia and America. The genus *Neurodromicius*, from the Miocene of North America, is provisionally referred by Professor Cope to this family; while *Laophis*, from the Tertiary of Salonica, has also been regarded as a member of the same group.

Ordinal Position Uncertain.—It will be convenient to mention here two imperfectly known genera from the English Purbeck, of which the ordinal position cannot at present be determined. They were regarded by Sir R. Owen as belonging to the Lacertilia, but their teeth are much more of a Dinosaurian type. The first genus, *Nythetes* (*Nuthetes*), is represented by a species of the size of some of the existing *Varanidæ*, but has teeth closely resembling those of the *Megalosauridæ*, although it is said that they were not implanted in distinct sockets, and were anchylosed to the bone. The second genus, *Echinodon*, is a smaller form, in which the teeth present a striking resemblance to the much larger ones of the Dinosaurian genus *Scelidosaurus;* they were implanted in imperfect sockets.

Here also may be mentioned the remarkable genus *Atoposaurus*, from the Kimeridgian lithographic limestones of Bavaria, which includes two species of small Lizard-like Reptiles, presenting the

following peculiar features. The manus seems to be of a Rhynchocephalian type; but the pes has only four digits, in which the phalangeals number 2, 3, 4, 4, or the same as in the Crocodilia. The proximal bones of the carpus are also elongated, as in that order; and the radius and ulna in the pectoral, and the tibia and fibula in the pelvic limb, are respectively in close apposition. The mandibular symphysis is long; and the dentition is said to resemble that of the *Geckonidæ* among the Lacertilia. The above characters point to a curious blending of Squamatine and Crocodilian features.

Fig. 1051, *bis*.—The African Cobra (*Naia haje*). Reduced.

CHAPTER LV.

CLASS REPTILIA—continued.

Orders Dinosauria, Crocodilia, and Ornithosauria.

Archosaurian Branch. — The three orders constituting this branch comprise the most highly developed of all Reptiles, and those which make the nearest approach in their organisation to the Avian type. They also include the largest forms yet known, not only among Reptiles, but also among all Vertebrates adapted for a life on land. The following features are common to the entire branch. The teeth are very generally implanted in distinct sockets; are never anchylosed to the bones of the jaws; and are exclusively confined to the premaxilla, maxilla, and dentary bones. Both the pectoral and pelvic limbs are always well developed; the cranium has no parietal foramen, but is furnished with both a superior and an inferior temporal arcade (as is shown in the figure of the Crocodilian skull on p. 1181); the quadrate is firmly fixed among the adjacent bones; and there is frequently no columella. The anterior ribs have a distinct capitulum and tuberculum; the dorsal vertebræ carry long transverse processes, which may be placed entirely on the arch; and there may be more than two vertebræ in the sacrum. There is never a T-shaped interclavicle, and the only indication of the precoracoid is afforded by the fontanelle in the coracoid, which indicates its original duality. The humerus has no foramen, but an ectepicondylar groove may occur. The proximal row of the tarsus comprises two bones, representing the astragalus and calcaneum. Abdominal ribs are generally present. The number of phalangeals in the limbs approximates more or less closely to that obtaining in the Streptostylic branch, although in some cases there is a reduction. The lateral surface of the mandibular ramus may have a vacuity. As a rule the centrum of the atlas vertebra forms an odontoid process more or less closely attached to the centrum of the axis; the arch of the former being

supported by the crescent-shaped first intercentrum. Generally the second intercentrum, like that of Birds, was likewise fused with the centrum of the axis; but in one Dinosaur (? *Megalosaurus*) this element exists as a distinct wedge-like bone.

In the pelvis the pubis and ischium never form the broad and flattened plates found in the Synaptosaurian branch, and they frequently assume a more or less rod-like form with expanded extremities (fig. 1073). The ilium (*ibid.*) frequently presents an expanded form; and the obturator notch is never converted into a foramen.

Order VIII. Dinosauria.—The Dinosaurs comprise the largest land Reptiles; and while some of them approximate closely to the type of structure obtaining in Birds, others come so near to the more generalised Crocodilians that it is almost impossible to give any definition of the order that will separate it from the latter. It is, indeed, probable that in the Lower Trias there lived the common ancestors of the two orders, and the forms from the upper division of the same period indicate not only the close connection between these two groups, but also show some signs of affinity with the Rhynchocephalia.

It has recently been proposed to divide the Dinosauria into two orders, from the structure of the pelvis, for which the names Ornithischia and Saurischia have been proposed. If, however, this view be eventually accepted, it would be advisable to adopt the name Ornithopoda for the first division, and to restrict the term Dinosauria to the second, which would include the two groups here termed Theropoda and Sauropoda. In regard to the names of the suborders, it should be mentioned that Professor Cope first proposed the names Orthopoda and Goniopoda for the groups here termed Ornithopoda and Theropoda, on the ground that the relations of the tibia and fibula were essentially different in the two. According, however, to Professor Huxley, this alleged difference does not exist, and these names are therefore rejected by him.

This order is entirely extinct, and may be regarded as characteristic of the Mesozoic period; since it ranges from the Trias to the Uppermost Cretaceous of Maastricht, and the Laramie beds of the United States, and appears to have attained its maximum development in the Jurassic and Wealden. In space this order was widely distributed over Europe and North America; and it has also been met with in India and Africa.

Dinosaurs vary exceedingly in the contour of the body and limbs; which in some instances were more or less of a crocodilian type, but in others approach very markedly to the avian structure; the latter feature being most marked in the pelvis and hind limbs. The hind limbs were either moderately or excessively long; while the body

was sometimes defended by a bony dermal armour, which may carry long spines, but apparently was never composed of imbricating pitted scutes. The centra of the vertebræ are very generally amphicœlous; but are not unfrequently opisthocœlous in the cervical, and more rarely in the anterior dorsal region; and occasionally some of the caudals are procœlous. The neuro-central suture was usually persistent till an advanced period of life. As a general rule the sacrum includes from three to six vertebræ, but occasionally the number is reduced to two. The cervical ribs are not produced into spines directed antero-posteriorly; and there are no uncinate processes to the ribs. The rib-facets of the middle dorsal vertebræ may either form a "step" on the transverse process, as in the Crocodilia, or may be placed on the lamina of the arch. The skull has many features of that of the earlier Crocodilia, but also seems to approximate in some cases to the Rhynchocephalian type. The premaxillæ were but rarely fused together; and the union of the mandibular rami in the symphysis is cartilaginous. The teeth are generally more or less laterally compressed, frequently having serrated edges, and may be of complex structure; they were not always implanted in distinct sockets. The sternal region is imperfectly known, but it frequently comprised two paired bones, which may represent parts of the sternum. The limb bones may be either solid or furnished with a medullary cavity. The coracoid has a fontanelle, and is always short and rounded. In the pelvis (fig. 1060) the ilium has both the pubic and preacetabular processes well developed, the latter being in some cases greatly elongated; the pubis always takes a share in the formation of the acetabulum (of which the inner wall is unossified), and may be directed either forwards or backwards. The femur may have its head placed either obliquely (as in the Crocodilia) or at right angles to the condyles; and may or may not be furnished with an inner trochanter. The tibia, as in Birds, had a cnemial crest; and the astragalus was frequently flattened, and more or less closely applied to the lower end of the tibia.

Suborder 1. Ornithopoda.—This suborder is taken to include the Stegosauria of Professor Marsh, and embraces the most specialised forms. In the skull (figs. 1059, 1062) the anterior part of the premaxilla is devoid of teeth; there is no preorbital vacuity; the nares are placed at the extremity of the skull; and the teeth are more or less complex, and are frequently not set in distinct sockets. The vertebræ are solid throughout. The pectoral limb is considerably shorter than the pelvic; the limb bones may be either solid or hollow. The ilium generally has its preacetabular process much elongated (fig. 1060), although this is not the case in the type of *Camptosaurus* (fig. 1052), the ischium has an obturator process;

but the most striking and remarkable feature in the group, and one in which it differs from all others except Birds, is that the shaft of the pubis is directed backwards more or less nearly parallel with the ischium, while a shorter and thicker portion in advance of the acetabulum projects forwards. How remarkably this pelvic structure approximates to that of Birds may be seen by comparing figs. 1052 and 1060 with that of the pelvis of a Ratite Bird given in the sequel. Thus the large preacetabular process of the pubis of the Dinosaur corresponds with the much smaller but similarly situated

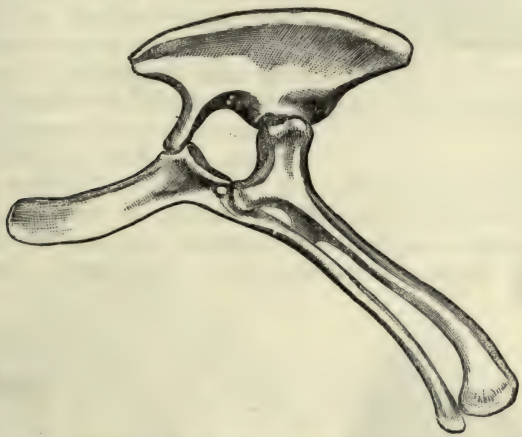

Fig. 1052.—The left side of the pelvis of *Camptosaurus dispar;* from the Upper Jurassic of North America. One-twelfth natural size. The upper bone is the ilium, that on the left the pubis, and that on the right the ischium. (After Marsh.)

pectineal process in the pelvis of the Ratite Birds (fig. 1107). In some cases the pubis had no median symphysis. All the more specialised members of the suborder appear to have walked habitually on the hind limbs alone. In this and the following suborder the length of the tibia is often nearly equal to that of the femur; and in *Hysilophodon* and *Compsognathus* the former bone, as in Birds, is the longer of the two.

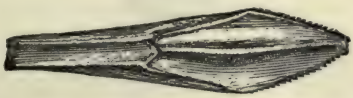

Fig. 1053.—Tooth of *Trachodon Foulki;* from the Upper Cretaceous of New Jersey. (After Leidy.)

Family Trachodontidæ. — The most specialised, as well as one of the most recent, families of the suborder, seems to be that typically represented by the genus *Trachodon* (*Hadrosaurus*). This family, although closely related to the next, is distinguished by having the teeth arranged in a number of vertical columns and articulating together so as to

form a kind of pavement. The type genus, of which a tooth is shown in fig. 1053, was first described from the Upper Cretaceous of the United States, but has been subsequently recorded from the Upper Greensand of Cambridgeshire. All the dorsal vertebræ are opisthocœlous. Five other genera—viz., *Diclonius*, *Cionodon*, *Monoclonius*, *Dyscanus*, and *Agathaumas* — from the Laramie beds of North America present a similar type of dentition, and have been referred to the same family; the first being probably identical with *Trachodon*. The Laramie beds, it should be observed, appear to be transitional between the Cretaceous and Eocene although referable to the former epoch. In the so-called *Diclonius* the skull, although presenting many of the features of that of *Iguanodon*, is much more elongated and depressed, and has the edentulous premaxillæ produced in advance of the large nares. *Orthomerus*,

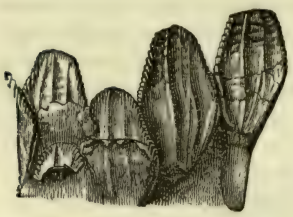

Fig. 1054.—Four lower teeth of *Iguanodon* in the jaw. Reduced.

A B

Fig. 1055.—Inner (A) and outer (B) aspects of a lower tooth of *Iguanodon bernissartensis*; from the Wealden of Sussex.

of the Upper Cretaceous of Maastricht in the Netherlands, may probably be also referred to this family, although it shows some signs of connection with the next.

Family Iguanodontidæ.—The characteristic features of this remarkable family are to be found in the hollow limb bones; the

slenderness and relative length of the pubis and ischium (figs. 1052, 1060); the avian characters of the femur, which has a large inner trochanter; the digitigrade hind-foot, furnished with either three or four digits and more or less elongated metatarsals; and the short pectoral limbs. The bones usually referred to the sternal region are typically hatchet-shaped, and have been regarded by some authorities as clavicles, although it seems more probable that they are connected with the xiphisternum. The cervical vertebræ were usually opisthocœlous; and the rib-facets in the middle dorsal region were placed on the arch. The teeth (figs. 1054, 1055) were arranged in a single row, and are very peculiar and characteristic. Thus they have flattened, diamond-shaped crowns, bearing strongly-marked serrations on the anterior and posterior borders, and one

Fig. 1056.—*Iguanodon bernissartensis*. The skeleton; from the Wealden of Belgium. About $\frac{1}{15}$ natural size. The scale indicates metres. (After Dollo.)

or more vertical ridges, some of which may themselves be serrated, on their outer aspect. The mandible, again, presents the peculiar feature of having a horse-shoe-like predentary bone at the extremity of the symphysis (fig. 1059). This predentary ossification is devoid of teeth; while the mandibular symphysis itself is deeply channelled. The family ranges from the Middle Jurassic to the Wealden and Neocomian of Europe; its members generally showing a gradual increase in size from the lower to the higher horizons. Like the members of the preceding family, the Iguanodonts habitually supported themselves on the hind limbs, as in the accompanying figure.

In the imperfectly known *Sphenospondylus* of the English Wealden, the anterior dorsal vertebræ were opisthocœlous, and all the dorsals had very low neural arches. In the type genus *Iguanodon*, which includes the largest forms, the skull (fig. 1059) is comparatively short, with large and terminal nares and no teeth in the premaxilla. In the typical forms, constituting the Euiguanodont group, the dorsal vertebræ (fig. 1058) are amphicœlous, those in the anterior part of the series having very tall neural arches and compressed centra; while the sacral vertebræ are anchylosed together, and have rounded inferior, or hæmal, surfaces. In the pelvis (fig. 1056) the ilium is shallow, with a sharply pointed post-acetabular process; while the pubis is much shorter than the

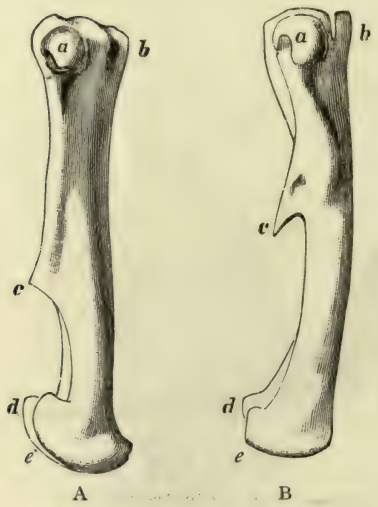

Fig. 1057.—Inner aspect of the left femur of *Iguanodon bernissartensis* (A), and of *Camptosaurus Leedsi* (B). Reduced to same size. *a*, Head; *b*, Lesser trochanter; *c*, Inner do.; *d*, Ectocondyle; *e*, Entocondyle.

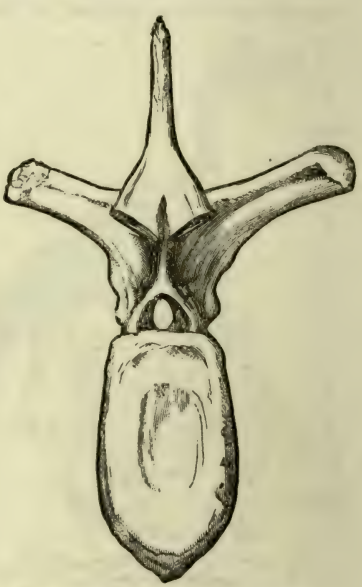

Fig. 1058.—Posterior aspect of anterior dorsal vertebra of *Iguanodon bernissartensis*; from the Wealden of the Isle of Wight. One-sixth natural size. (After Seeley.)

ischium (which is twisted on itself), and does not form a symphysis. The femur (fig. 1057, A) is characterised by the inner trochanter (*c*) forming a crest directed almost immediately backwards, while its shaft is nearly straight. The foot had only three functional digits, of which the metatarsals were short and thick, and the phalangeals broad and flat; while in the manus the one phalangeal of the first digit, or pollex, was modified into a stout conical spine. As in the other members of the family, the astragalus, although not

anchylosed to the tibia, was closely applied to its distal extremity, and thus rendered the structure of the ankle-joint (as in many other members of the order) essentially similar to that of a Bird.

It may be observed that the inner trochanter of the femur corresponds to the small one found in some Birds, which gives attachment to the femoro-caudal and ischio-femoral muscles, and it is interesting to find, from the observations of M. Dollo, that its form in *Iguanodon* is that which agrees with the Avian type.

Iguanodon ranges from the Wealden to the Lower Greensand, and hitherto has only been described from Europe. The two representatives of the typical or Euiguanodont group occur in the Upper Wealden and Lower Greensand, and comprise *I. Mantelli*, and the larger *I. bernissartensis* (fig. 1056); these two species being also distinguished from one another by the number of the sacral vertebræ, and the contour of the ilium and femur.

The length of the entire body of the larger *I. bernissartensis* is estimated at about 33 feet. The history of the gradual reconstruction of the skeleton of this genus affords an instructive instance of the results which may be attained by careful and patient study of fragmentary remains.

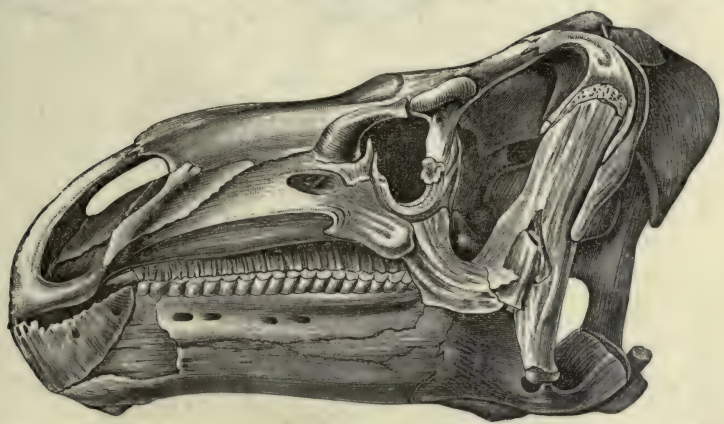

Fig. 1059.—Left lateral aspect of the skull of *Iguanodon bernissartensis;* from the Wealden of Belgium. Much reduced. The anterior aperture is the nares; the middle one the orbit; and the posterior the infratemporal fossa. The predentary bone is seen at the extremity of the mandible. (After Dollo.)

By the labours of the late Dr G. Mantell of Lewes, in the first half of this century, a considerable knowledge was acquired of the greater part of the skeleton, although the structure of the pectoral and pelvic girdles remained a puzzle. The structure of the latter was, however, after more than one ineffectual attempt, finally solved by the labours of Professor Huxley and Mr J. W. Hulke.

In the Wadhurst Clay, or Lower Wealden, of Sussex, we meet with three species of *Iguanodon* which connect the preceding typical

forms with the undermentioned genus *Camptosaurus*. *I. Dawsoni* is a form intermediate in size between *I. Mantelli* and *I. bernissartensis*, characterised by the less compressed centra and lower arches of the dorsal vertebra; and also by the form of the ilium (fig. 1060, *Il*), which is of great depth, and has a deep and rounded postacetabular process, while the preacetabular process has a horizontal inferior plate. In the smaller *I. Fittoni* the ilium is equally deep, but has the postacetabular portion narrowed to a point laterally, with a distinct inferior horizontal plate; while the sacrum has laterally com-

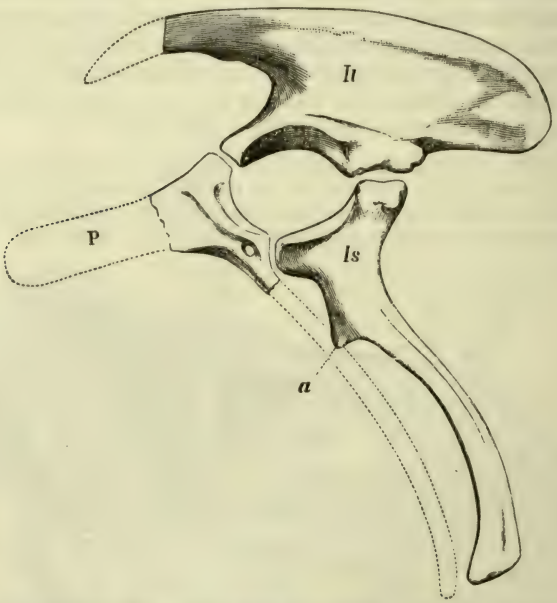

Fig. 1060.—Left pelvic bones of Lower Wealden Iguanodons. One-sixteenth natural size. *Il*, Ilium of *Iguanodon Dawsoni*; *P*, Imperfect pubis of do.; *Is*, Ischium of *I. hollingtoniensis*; *a*, Obturator process of ischium.

pressed vertebræ like those of *I. Mantelli*. The posterior portion of the ilium of this species is indeed almost indistinguishable from that of *Camptosaurus* (fig. 1052). Finally, in *I. hollingtoniensis*, which agrees approximately in the proportions of the limbs with *I. Mantelli*, the femur had a curved shaft and pendant trochanter as in *Camptosaurus* (fig. 1057, B); while the sacrum had the vertebræ remaining separate from one another, with their inferior surfaces flattened, as in that genus, with which this species also agreed in the contour of the ischium (fig. 1060, *Is*), which has a stout shaft not twisted upon itself. This species agreed, however,

with the typical species of the genus in having the pollex modified into a conical spine, and thereby differed from *Camptosaurus*, although indicating how the one genus passed into the other. It is not improbable that the large Iguanodont from the Upper Jurassic of the United States, described as *Camptosaurus amplus*, should be referred to this group of *Iguanodon*, since it has but three functional digits in the pes.

With the genus *Camptosaurus* (*Camptonotus*), we come to forms which are usually of smaller size than the preceding. It occurs typically in the Upper Jurassic of North America; but certain forms, from the English Oxford and Kimeridge Clays, to the latter of which the name *Cumnoria* has been applied, as well as a Wealden species, do not appear to be generically separable. This genus has teeth of somewhat simpler structure than those of *Iguanodon*, and is further characterised by the flattened hæmal surfaces of the centra of the sacral vertebræ, which appear to have remained separate throughout life; by the short preacetabular process of the ilium (fig. 1052) of the type species; by the equality in the length of the pubis and ischium; by the pendant, or downwardly directed, inner trochanter of the curved femur (fig. 1057, B); and the presence of five digits of normal structure in the manus, and typically of four in the pes. The length of the femur of the type species is some 21 inches. The English forms are not fully known; but so far as this is the case they agree in essential characters with the type: the structure of the manus and pes is, however, unfortunately unknown. *C. Leedsi*, of the Oxford Clay, is known only by the femur (fig. 1057, B), which measures a little over one foot in length; while in the Kimeridgian *C. Prestwichi* (the type of *Cumnoria*) we are acquainted with the greater part of the vertebral column, in which the dorsals have tall neural arches, while the ilium has a long preacetabular process like that of *Iguanodon*. The Wealden *C. valdensis* is typified by a femur. *Laosaurus* is an allied form from the Upper Jurassic of the United States, distinguished by its amphicœlous cervical vertebræ. The imperfectly known *Cryptodraco* (*Cryptosaurus*), from the Oxford Clay of England, is characterised by the great stoutness of the femur, which exceeds a foot in length, and has a straight shaft, with an inner trochanter like that of *Iguanodon bernissartensis*, but differs from the corresponding bone of all other members of the family in the absence of a groove on the anterior aspect of the lower end between the condyles.

Lastly, we come to the consideration of *Hypsilophodon*, the smallest and least specialised representative of the family, which is now well known to us through the labours of Mr J. W. Hulke. In this genus, which occurs in the Upper Wealden of England, the general structure of the pelvis, as well as the pendant inner tro-

chanter of the femur, resemble the corresponding elements of *Camptosaurus*; and there are likewise four functional digits in the pes, of which the metatarsals are elongated; while the teeth, which also occur in the hinder half of the premaxilla, are somewhat simpler than those of *Iguanodon*. In conclusion, we may mention two imperfectly known forms which are evidently related to this family. Of these, *Mochlodon*, from the Upper Greensand of Austria, is characterised by the absence of the channelled mandibular symphysis characteristic of typical forms; while *Craspedodon*, from the Upper Cretaceous of Belgium, is a very small Dinosaur, merely known by its teeth, which are more complex than those of *Iguanodon*.

Family Scelidosauridæ.—This family includes a group of remarkable Dinosaurs of medium dimensions, characterised by being clad in a stout dermal armour, usually consisting of detached scutes and long spines, but sometimes taking the form of a solid carapace completely covering the lumbar region. The rami of the mandible are slender and tapering, but it is not known whether a predentary bone was present. The teeth (fig. 1061) have laterally flattened and subtriangular crowns, with the borders carrying serrations set more or less obliquely or parallel to the long axis of the tooth. The anterior and middle dorsal vertebræ differ from those of the *Iguanodontidæ* in having the articulation for the head of the rib forming a "step" on the transverse process, as in Crocodiles, and not a facet on the arch; while there is also no fossa between the transverse process and the postzygapophysis. The limb-bones are solid and massive; the pre- and postacetabular processes of the ilium very long; and the pubis and ischium comparatively short. The femur has an inner trochanter; the metatarsals are short and thick; and the pes, which was probably plantigrade, always has four functional digits. This family connects the *Iguanodontidæ* with the *Stegosauridæ*, and appears to be confined to the Old World, ranging from the Lias to the Cretaceous.

Fig. 1061.—Tooth of *Scelidosaurus Harrisoni*; from the Lower Lias of Dorsetshire. Twice natural size.

The type genus *Scelidosaurus*, of which a tooth is shown in fig. 1061, occurs in the Lower Lias of Dorsetshire; and is well characterised by the strongly-marked serrations of the teeth, and the short and conical dermal spines or scutes. In the Wealden, the well-known *Hylæosaurus* was a Dinosaur of considerable dimensions, characterised by its enormous and laterally-compressed dermal spines, but of which the skull and teeth are unfortunately still unknown, certain detached teeth which have been provisionally referred to it being

now known to be Sauropodous. The anterior dorsal vertebræ have a well-marked hæmal ridge, which disappears in those later in the series.

Regnosaurus is founded upon a lower jaw from the Wealden, which may pertain either to the last or the following genus. In *Polacanthus*, of the same beds, we have a remarkable form, in which the dermal armour constitutes a completely solid carapace over the whole of the dorsal aspect of the lumbar region, some of the component scutes being tuberculated, and others ridged; while there was also a number of detached flattened spines somewhat like those of *Hylæosaurus*, which probably formed a line in the dorsal region. This peculiar type of carapace forcibly recalls that of the Glyptodont Edentates. In the Chalk-Marl and Cambridge Greensand, we find *Acanthopholis* with a dermal armour somewhat similar to that of *Scelidosaurus*, but with rather more complex teeth. The smaller *Anoplosaurus*, of the Cambridge Greensand, was probably a closely allied, if not generically identical, form; while the equally small *Syngonosaurus* and *Eucercosaurus*, of the same deposits, are distinguished by their compressed and carinated dorsal vertebræ, which resemble those of *Hylæosaurus*. Apparently allied to these forms is *Vectisaurus*, of the Wealden of the Isle of Wight, originally referred to the *Iguanodontidæ*, but showing the "step" on the transverse processes of the dorsal vertebræ characteristic of the present family. *Priodontognathus*, founded on a fragment of jaw of unknown age, is probably referable to one of the preceding forms.

Family Stegosauridæ.—This family is typically represented by the genus *Stegosaurus;* but before mentioning that form it will be convenient to refer to two apparently allied Dinosaurs from the Karoo system of the Cape, both of which are very imperfectly known, and may indicate a family connecting the present with the *Iguanodontidæ*. In *Euscelesaurus* (more correctly *Euscelidosaurus*), as the first of these forms is named, the limb-bones were solid, and the femur has a large inner trochanter, and approximates somewhat to that of the Iguanodonts. The tibia and fibula seem, however, to have been more like those of the *Stegosauridæ;* being anchylosed at their two extremities, and closely joined to the astragalus and calcaneum. The caudal vertebræ, belonging either to this or the next genus, are of an Iguanodont type. The genus *Orinosaurus* (*Orosaurus*) was founded upon a bone of a larger reptile, regarded by its describer as the distal end of a femur, but which is really the proximal end of a tibia. Although solid throughout, this bone resembles the tibia of *Iguanodon* in its expanded extremity, and thus suggests a transition between the *Iguanodontidæ* and *Stegosauridæ*.

The genus *Stegosaurus* was originally described from the Upper

Jurassic of North America; but it appears that certain forms from the Oxford and Kimeridge Clays of England, described at an earlier date under the preoccupied name of *Omosaurus*, are not entitled to generic distinction. These Dinosaurs agree with the *Scelidosauridæ* in the general structure of their teeth, and the possession of a dermal armour of scutes and spines, as well as in their solid limb-bones; but differ by the great height of the neural arches of the vertebræ, as well as by the circumstance that in the sacrum each arch is either chiefly or entirely supported by a single centrum, instead of by the adjacent portions of two centra, as in the preceding families. The skull (fig. 1062) shows many points of resemblance to that of *Iguanodon*, especially in the presence of a predentary bone; but it is lower and narrower, and thereby approximates to the Scelido-

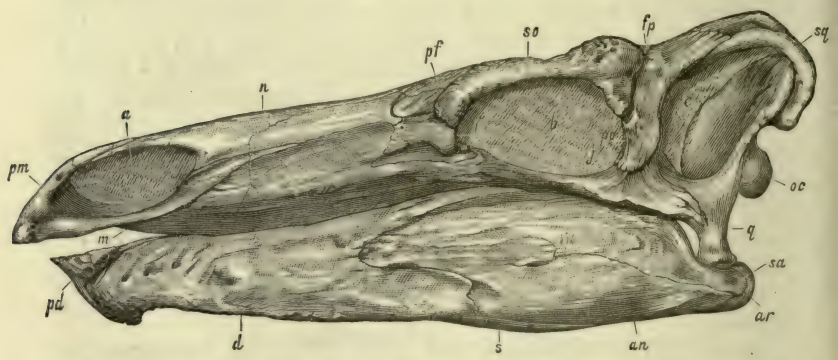

Fig. 1062.—Left lateral view of skull of *Stegosaurus stenops;* from the Upper Jurassic of North America. One-quarter natural size. *a*, Nares; *b*, Orbit; *c*, Infratemporal fossa; *pm*, Premaxilla; *m*, Maxilla; *n*, Nasal; *pf*, Prefrontal; *so*, Supraorbital; *fp*, Postfrontal; *po*, Postorbital; *l*, Lachrymal; *j*, Jugal; *q*, Quadrate; *sq*, Squamosal; *oc*, Occipital condyle; *ar*, Articular; *sa*, Surangular; *an*, Angular; *s*, Splenial; *d*, Dentary; *pd*, Predentary. (After Marsh.)

saurian type. The Iguanodont resemblance is, however, so marked as to forbid the reference of the forms with dermal armour to a separate suborder. The two rami of the caudal chevron-bones do not unite superiorly. In the pelvis (fig. 1063) the ilium has an enormous preacetabular process, and a very short postacetabular portion; while the ischium and pubis are relatively short. In the femur (fig. 1063) the inner trochanter is either very small or absent; the metatarsals are very short and stout; and the five digits of the plantigrade pes approximate in contour to those of the Elephant. The tibia and fibula are suturally united together at their extremities; and the former is completely joined to the astragalus, and the latter to the calcaneum. Other peculiar features of these remarkable reptiles are to be found in the structure of the

neural canal in the sacrum. In the solid structure and general contour of the limb-bones, as well as in the relations of the sacral centra to their arches, *Stegosaurus* approximates to the sub-order Sauropoda; and thus shows how impossible it is to bring out the true relationships of animals in a linear classification. The type species indicates a reptile about two-thirds the dimensions of *Iguanodon bernissartensis*. The American species have no inner trochanter to the femur. The name *Diracodon* has been applied to an American Jurassic type characterised by some modification in the structure of the foot. *Dystrophæus*, from the Trias of Arizona, appears to be more or less closely allied to the *Stegosauridæ*.

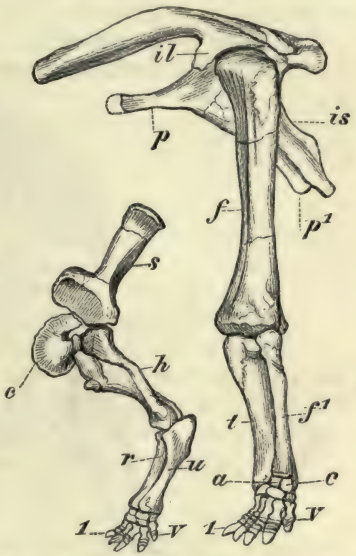

Fig. 1063.—The left pectoral and pelvic girdles and limbs of *Stegosaurus ungulatus*; from the Upper Jurassic of North America. $\frac{1}{24}$ natural size. *s*, Scapula; *c*, Coracoid; *h*, Humerus; *r*, Radius; *u*, Ulna; *i–v*, Phalangeals; *il*, Ilium; *is*, Ischium; *p*, *p*¹, Pubis; *f*, Femur; *t*, Tibia; *f*¹, Fibula; *a*, Astragalus; *c*, Calcaneum. (After Marsh.)

Family Ceratopidæ.—This name has been proposed for some remarkable Cretaceous Dinosaurs allied to the preceding family, but can only be provisionally adopted. The type genus *Ceratops* (according to Cope identical with his *Polyonax*), of the Laramie Cretaceous of the United States, carries a pair of large horn-cores on the skull, which are curiously like those of the *Bovidæ*, and were probably sheathed with horn. The body was covered with dermal scutes, which not improbably had overlying horny shields like those of Chelonians. In the Upper Greensand of Austria there occur similar horn-like bones, once thought to have been attached to the body, and described as *Struthiosaurus* (*Cratæomus*), and it has yet to be shown that the American types are generically distinct. A gigantic allied form, from the Laramie, has been christened *Triceratops*, and is characterised by the presence of an additional nasal horn-core, supported by the coalesced premaxillæ and an additional *rostral* bone. The skull is stated to be upwards of six feet in length; the frontal horn-cores measuring some 22 inches. A horn-core-like bone in the British Museum, from the Wealden, not improbably indicates an allied type.

Nodosaurus, of the Laramie, is a form more or less nearly allied to *Stegosaurus*, characterised by the completeness of the dermal armour, which consists of rows of rounded knobs, becoming small and quadrangular near the head. The skull is unknown.

Finally, the remarkable genus *Stenopelix*, from the German Wealden, should perhaps find a position somewhere in this neighbourhood, although it differs from all other members of this suborder by the presence of cavities in the centra of the caudal vertebræ.

Suborder 2. Theropoda.—The suborder Theropoda holds in some respects a position intermediate between the Ornithopoda

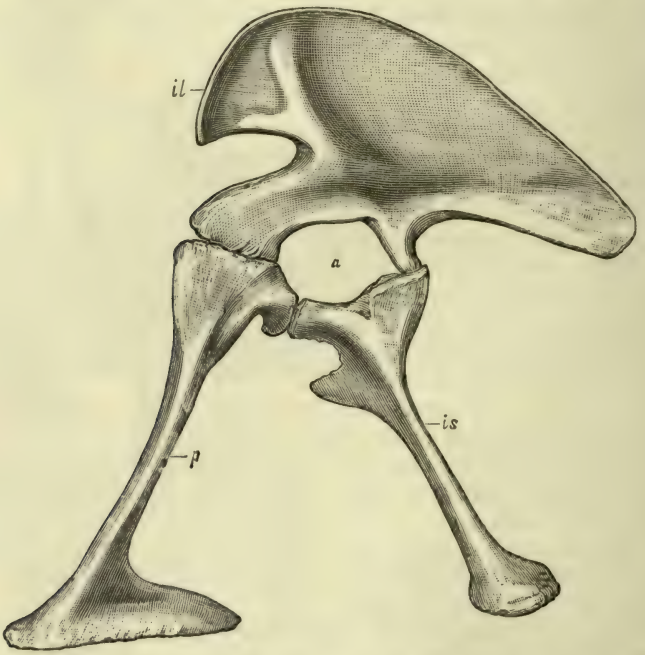

Fig. 1064.—The left side of the pelvis of *Allosaurus fragilis;* from the Upper Jurassic of North America. One-twelfth natural size. *il*, Ilium; *is*, Ischium; *p*, Pubis; *a*, Acetabulum. (After Marsh.)

and the Sauropoda, although its members are more nearly allied to the latter; with which, as already mentioned, it has been proposed to group them, under the name of Saurischia. In many respects, such as the structure of the teeth, the form of the femur, the occasional presence of only two sacral vertebræ, and the form of the quadrate bone, certain members of this suborder

make a nearer approximation than the Sauropoda to the generalised Crocodilia, although in their hollow limb-bones they agree with the higher Ornithopoda. All the forms were carnivorous. In the skull (fig. 1070) the premaxillæ are furnished throughout with teeth, which are laterally compressed (fig. 1065) and backwardly curved, with trenchant edges, of which the posterior, and frequently also the anterior, border is serrated; the directions of these serrations being generally nearly at right angles to the axis of the crown. These teeth are always implanted in distinct sockets; and the skull has a large preorbital vacuity (fig. 1070). The centra of all the vertebræ are hollowed internally; and their neural arches articulate by zygosphenes (diplosphenes) corresponding to those of the Squamata; while the centra (fig. 1067) are much compressed laterally. The limb-bones always have medullary cavities; and since the pectoral limb is much shorter than the pelvic, it is probable that many forms were of bipedal habits, although some may have been quadrupedal. In the pelvis (fig. 1064) the ilium is of great vertical depth, and has a short preacetabular process; while the pubis is directed downwards and forwards, and unites with its fellow in a long bony symphysis, which is generally extended up the anterior face of the two bones; thus causing them to have the appearance of an elongated Y, when seen from this aspect. Both the pubis and ischium are of a comparatively short and slender type of structure, and the latter usually has an obturator process like that of the Ornithopoda. The astragalus is usually closely applied to the tibia, and not unfrequently gives off a long flattened process lying on the anterior face of the latter bone, and thus resembles the condition found in young Ratite Birds before the anchylosis of the two bones has taken place. The metatarsals are elongated, and the feet digitigrade. In the manus the number of the digits varies from four to five; while in the pes there may be either three or five. And in all cases their terminal phalangeals are furnished with curved claws, which in the manus are very long and prehensile, and were apparently adapted for the seizure and retention of the living prey.

Fig. 1065.—Lateral aspect of a tooth of *Megalosaurus Bucklandi*; from the Stonesfield Slate. One-third natural size.

It may further be observed that while the cervical vertebræ are frequently shorter than the dorsals, as in the Ornithopoda, yet they are sometimes longer, like those of the Sauropoda; while the vertebral arches in the sacrum are occasionally supported by single centra, as in the latter. Finally, the femur, which may be either somewhat longer or shorter than the tibia, is generally of a more Crocodilian type—especially shown in its flattened head—than in

any other Dinosaurs, although it has a distinct inner trochanter. In all cases the dorsal vertebræ are amphicœlous.

Family Anchisauridæ.—The least specialised forms constituting this family, of which the name must be considered provisional, are mainly known from beds of Triassic age, and are typically represented by the North American genus *Anchisaurus* (*Amphisaurus*). The cervical vertebræ are amphicœlous; the pubes are slender rod-like bones; and there are five digits in both the manus and the pes. The teeth (fig. 1066) usually have comparatively thick and short crowns, with a slightly convex posterior border, and more or less oblique serrations, which occupy the whole of both borders. *Thecodontosaurus* occurs in the Lower Keuper near Bristol; the teeth of the type species being much smaller than the one figured in the woodcut. *Anchisaurus* (which, according to Professor Marsh, is identical with a form described at an earlier date under the preoccupied name *Megadactylus*) occurs in the reputed Trias of the United States; but no evidence has yet been presented to show how it differs from the European genus. The writer last quoted includes in this family the American Triassic genera *Bathygnathus* and *Clepsysaurus*, both of which are still very imperfectly known. Here may be mentioned the genus *Massospondylus*, from the Karoo system of South Africa and the Maleri stage of the Gondwana system of India, of which a tooth is shown in fig. 976 (p. 1049), and the centrum of a dorsal vertebra in fig. 1067. These vertebræ approximate to those of *Megalosaurus*, and have a fusiform internal cavity.

Fig. 1066. — Outer aspect of the crown of a tooth of *Thecodontosaurus platyodon*; from the Lower Keuper near Bristol.

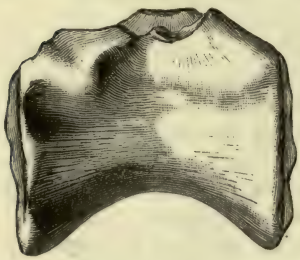

Fig. 1067.—Lateral and inferior aspects of the centrum of a dorsal vertebra of *Massospondylus carinatus*; from the Karoo system of Basutoland. One-half natural size.

Finally, it is highly probable that an amphicœlous cervical vertebra obtained from beds of unknown Mesozoic age in Bathurst Island, Arctic America, and described under the name of *Arctosaurus*, indicates a Dinosaur more or less closely allied to the present or following family. This vertebra agrees approximately in size with that of *Calamospondylus* (fig. 1071), but has free cervical ribs and a neural spine; the length and curvature of the

centrum being indicative of a long and arched neck. The occurrence of a Dinosaur so far north is of extreme interest, as serving to show how genera common to the Old and New Worlds may have migrated from the one hemisphere to the other.

Family Megalosauridæ.—In this family the cervical vertebræ are (when known) shorter than the dorsals, and may be either amphi- or opisthocœlous; while the dorsals often have prominent ridges at the base of the arches, between which are deep pits; the vertebral centra, as in the last family, having a fusiform internal cavity. In the pelvic limb of the type genus, the femur is of a remarkably Crocodilian type, and is longer than the tibia. The crowns of the teeth (fig. 1065) are more or less tall, and much compressed, with the posterior border distinctly concave, and the serrations, which are nearly at right angles to the axis of the crown, usually wanting at the lower part of the anterior border. In the Lower Keuper of England we meet with *Palæosaurus* (with which *Cladyodon* of the same deposits may be identical), of which only detached teeth are known. In the Upper Keuper of the Continent there occurs the comparatively generalised genus *Zanclodon* (*Teratosaurus*), which is not improbably identical with *Plateosaurus*, in which case the latter name should be adopted. The serrations on the anterior borders of the crowns of the teeth continue nearly to the base; the cervical vertebræ are amphicœlous; there are but two vertebræ in the sacrum; and the astragalus does not give off a process ascending on to the anterior surface of the tibia. One of the species was fully as large as *Megalosaurus*, and the genus was probably represented in the Lower Lias of Dorsetshire. The small *Epicampodon* (*Ankistrodon*), of the Panchet stage of the Indian Gondwanas, has teeth (fig. 1068) of a Megalosauroid type, in which the serrations are totally absent from the anterior border, and do not extend to the base of the posterior border.

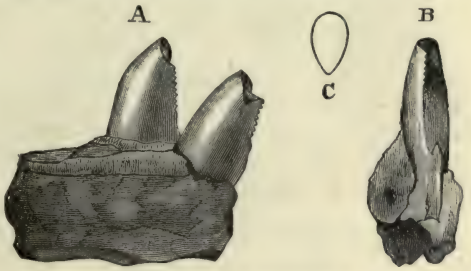

Fig. 1068.—Fragment of the mandible of *Epicampodon indicus;* from the Panchet beds of the Gondwanas. Three times natural size. A, Lateral; B, Posterior aspect; C, Transverse section of tooth. (After Huxley.)

The type genus *Megalosaurus* has been rendered classic through the labours of the late Professors Buckland and Phillips, and affords an excellent and instructive instance of the gradual restoration of the skeleton of an extinct and uncouth form from more or less fragmentary remains. In Europe this genus ranges from the Stones-

field Slate (Lower Jurassic) of England to the topmost Cretaceous of Maastricht in Holland; and has also been recorded from the Upper Cretaceous of Southern India. There is good evidence of the existence of two species in the Wealden. An attempt at a restoration of the skeleton of the type species is shown in the accompanying woodcut. The North American *Allosaurus* (of which the pelvis is represented in fig. 1064) appears to be a closely allied form of Upper Jurassic age. The nearly entire skeletons of the latter and other American forms have shown that certain very excusable errors were made in the restoration of the imperfect elements of the skeleton of the English genus; and it is quite evident that the skull of *Megalosaurus* must have had an inferior temporal arcade, and that it approximated more or less closely to that of *Ceratosaurus* (fig. 1070), although the bony processes of the latter may have been wanting. In the teeth (fig. 1065) the serrations on the anterior border are in

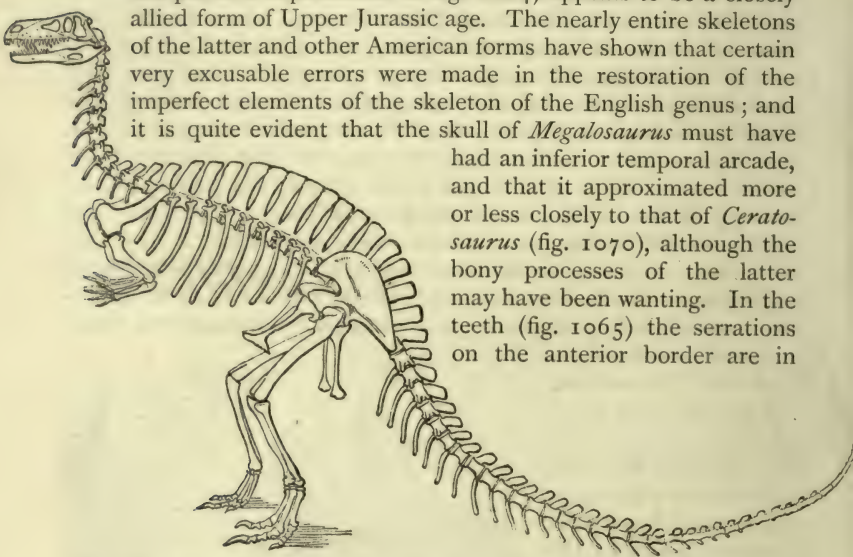

Fig. 1069.—Restoration of the skeleton of *Megalosaurus Bucklandi*; from the Stonesfield Slate. Greatly reduced.

some cases confined to the upper half of the crown, but in others extended nearly throughout. Typically there are five vertebræ in the sacrum; the cervical vertebræ are opisthocœlous; the astragalus has a process ascending on to the tibia; and there were three digits in the pes and probably four in the manus. In the North American *Creosaurus* we have an allied Upper Jurassic genus, in which the postcervical vertebræ have very deep depressions on the sides of their centra; and there are but two sacral vetebræ. In *Ceratosaurus*, of the Upper Jurassic of North America, the skull (fig. 1070) is remarkable for carrying a single bony protuberance behind the terminal nares, and a pair of similar protuberances directly in advance of the orbits; while the mandible has a lateral vacuity like that of the Crocodilia. Professor Marsh believes that the protuberances on the skull supported horns. In the type specimen the three pelvic bones and the metatarsals were respectively anchylosed

together; but this may perhaps be due to a pathological peculiarity of the individual. This genus is regarded by its describer as the type of a distinct family—the *Ceratosauridæ*. Here may be mentioned a small and imperfectly known Dinosaur from the Wealden for which the name *Aristosuchus* has been proposed. The type specimen comprises the sacrum and part of the pelvis. It is considered by its describer that the sacrum includes five vertebræ, while the pelvic bones, which have a long ventral symphysis, were originally described as pubes, although it has been subsequently suggested that they may be ischia. The dorsal vertebræ referred to this form by Sir R. Owen have a fusiform internal cavity in the centrum, but it has been recently suggested that this reference is

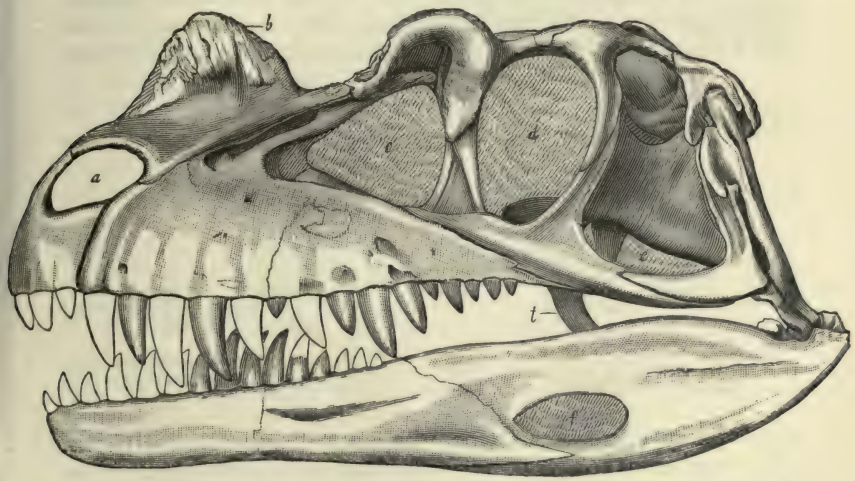

Fig. 1070.—Left lateral view of skull of *Ceratosaurus nasicornis*; from the Upper Jurassic of North America. One-sixth natural size. *a*, Nares; *b*, Bony prominence; *c*, Preorbital vacuity; *d*, Orbit; *e*, Infratemporal fossa; *f*, Mandibular vacuity; *t*, Transverse bone. (After Marsh.)

incorrect, and that this genus may have had dorsal vertebræ like those of the *Cœluridæ*, in which case this form may be referable to *Cœlurus*, in which, indeed, it has been placed by Professor Marsh.

Family Compsognathidæ.—This family is represented by the small *Compsognathus* of the Lower Kimeridgian Limestone of Bavaria, and the allied or identical *Hallopus* of the Upper Jurassic of North America. In the typical genus—known only by a single skeleton—the cervical vertebræ are opisthocœlous, and much longer than the amphicœlous dorsals, and have free cervical ribs. In the limbs the femur is shorter than the tibia, and both the manus and

pes have only three functional digits; the astragalus being closely applied to the tibia. The teeth and pelvis approximate to the Megalosaurian type. *Compsognathus* was about two feet in total length; and undoubtedly hopped on its pelvic limbs, after the manner of a bird. *Hallopus* is one of the few Dinosaurs with only two sacral vertebræ; the number of those of *Compsognathus* being unknown.

Family Cœluridæ.—This family is represented by comparatively small forms, ranging in size from five or six to about twelve feet in length. They are characterised by the vertebræ and ribs being completely honeycombed by cavities, communicating with a small aperture on the side of the centrum. The cervical vertebræ (fig. 1071) are typically longer than the dorsals, and have the ribs anchylosed to the arch and centrum, and the neural spine reduced to a mere ridge. The limb-bones are hollow, and the pelvis is of

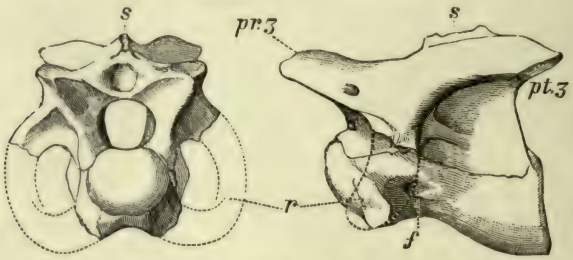

Fig. 1071.—Anterior and left lateral aspects of a cervical vertebra of *Calamospondylus Foxi*; from the Wealden of the Isle of Wight. Two-thirds natural size. *prz*, Prezygapophysis; *ptz*, Postzygapophysis; *r*, Rib (restored); *f*, Pneumatic foramen; *s*, Neural spine.

the ordinary Theropodous type, with a very long pubic symphysis. The type genus *Cœlurus*, typically from the Upper Jurassic of America, but also occurring in the English Wealden, has the cervical vertebræ greatly elongated, the first few being opistho- and the remainder amphicœlous. In *Calamospondylus* (fig. 1071) the cervicals were shorter, and were probably all opisthocœlous; the one known species being from the English Wealden. Professor Cope includes in this family other small Dinosaurs from the Trias of North America, which he identifies with *Tanystrophæus*, originally described on the evidence of extremely elongated caudal vertebræ from the German Muschelkalk, once referred to the Sauropterygia. In these forms all the cervical vertebræ were amphicœlous; and the femur has an inner trochanter. *Megadactylus*, which Professor Cope regards as identical with these forms, is, as already mentioned, identified by Professor Marsh with *Anchisaurus*.

Suborder 3. Sauropoda.—With the third and last suborder we

enter upon the consideration of the largest known Dinosaurs, and those which make so many marked approximations to the more generalised Crocodilia as to show how close is the relationship between that order and the Dinosauria.[1] The skull (fig. 1076) agrees with that of the Theropoda in having the premaxillæ completely toothed, and also in the presence of a large preorbital vacuity; but the external nares formed long slits in the fore part of the skull as in Ornithosaurs and Birds. The teeth are invariably set in distinct sockets and are of a spatulate form, without marginal serrations (fig. 1072). The sternal bones are ovate. All the vertebræ in advance of the sacrum, and sometimes those of that region also, have a large vacuity on each side of the centrum communicating with a series of internal cavities, which give a honeycomb-like structure to the whole vertebra. This affords a combination of strength and lightness in the massive supports necessarily required for the huge ribs, limbs, and muscles, which could not have been attained in any other manner. All the anterior vertebræ are opisthocœlous; and in the cervical region the ribs are anchylosed to the vertebræ, which have no neural spines, and are longer than the dorsals; while the spines of the latter are laterally expanded; and in the sacrum each centrum supports its own arch. The limb bones are solid; and since the pectoral limb is not much shorter than the pelvic, it appears that these Reptiles were habitually quadrupedal. All the feet were plantigrade, and furnished with five digits; those of the pes being terminated by large curved claws. The ilium (fig. 1073) has its upper border only moderately arched and its postacetabular portion short; while the pubis (fig. 1073), which is directed downwards and forwards, is stout with a comparatively small distal expansion, where it unites by a cartilaginous symphysis with its fellow of the opposite side. The ischium (fig. 1073) is likewise a stout bone agreeing with that of the Crocodilia in the absence of an obturator process; and the two ischia have a peculiar incurving of their distal extremity where they meet in a symphysis.

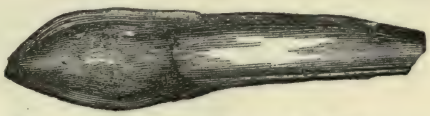

Fig. 1072.—Outer side of a tooth of *Morosaurus grandis*; from the Upper Jurassic of North America. One-half natural size. (After Marsh.)

It may be observed that in the lateral views of the pelvis shown in the figures, where the bones are drawn more or less nearly in a vertical plane, it is impossible to give a true idea of the peculiar contour of the distal extremity of the pubis and ischium. These bones are really concave from above downwards on the outer (figured) aspect, and convex on

[1] Professor Cope would include the Sauropodous Dinosaurs in the Crocodilia.

the inner aspect; and owing to a confusion between the proper inner and outer sides of the English specimens, only recently cleared up, it has been considered by some palæontologists that there was an essential difference between the structure of the pelvis of the English and American forms.

The femur in its straight shaft and absence of an inner trochanter likewise resembles to a considerable extent that of the Crocodilia;

Fig. 1073.—The left side of the pelvis of *Brontosaurus excelsus*; from the Upper Jurassic of North America. One-sixteenth natural size. *a*, Acetabulum; *il*, Ilium; *is*, Ischium; *p*, Pubis; *f*, Foramen in do. (After Marsh.)

although its head is not laterally compressed to the same extent, nor placed so obliquely to the distal condyles.

In time this suborder ranges from the Upper Trias to the Cretaceous, and it is especially well represented in the Kimeridge Clay and Wealden of Europe.

Family Atlantosauridæ.—This name may be provisionally adopted for a family which is represented by the genera *Atlantosaurus*, *Apatosaurus*, and *Brontosaurus*, of the Upper Jurassic of North America, as well as by allied European types. In these huge forms the ischium (fig. 1073) is directed downwards, and its shaft is thick and not bent upon itself; while the humerus is comparatively slender; and the chevrons of the caudal vertebræ have their superior extremities united. The teeth have the summit of the crown not

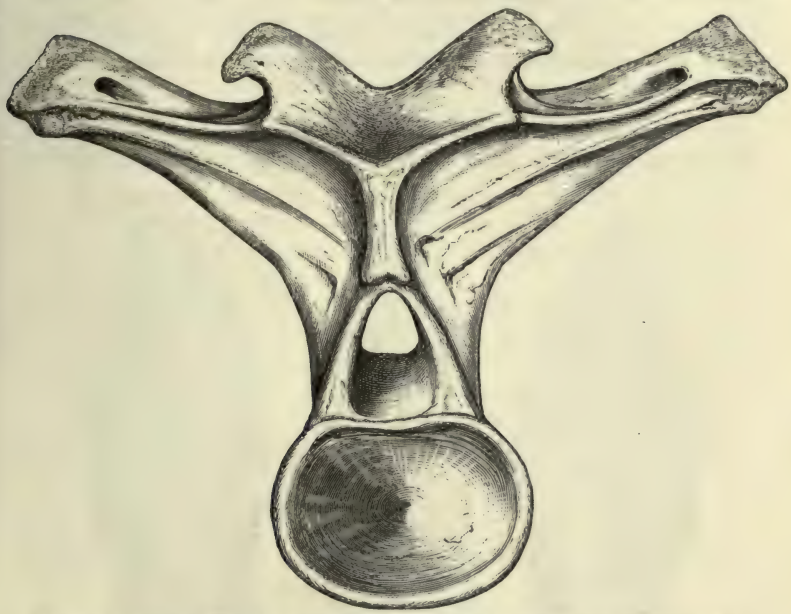

Fig. 1074.—Posterior view of an anterior dorsal vertebra of *Camarasaurus supremus*; from the Upper Jurassic of North America. Reduced. (After Cope.)

much incurved. Apparently closely allied to, if not identical with, some of the above-mentioned genera are *Amphicœlias* and *Camarasaurus* of the same formations. An anterior dorsal vertebra of the latter genus is represented in the accompanying woodcut; this vertebra is transitional between the cervicals and later dorsals, the neural spine of the latter being absent.

Professor Marsh estimates the total length of *Brontosaurus* at upwards of fifty feet, and its weight at more than twenty tons; and *Pelorosaurus*, of the English Wealden, must have been fully equal to these dimensions. In respect of the former, the learned American palæontologist observes, "that the animal at times assumed a more erect position than is represented in the restoration is probable, but locomotion on the posterior

limbs alone was hardly possible. The head was remarkably small. The neck was long, and, considering its proportions, flexible; and was the lightest portion of the vertebral column. The body was quite short, and the abdominal cavity of moderate size. . . . Each footprint must have been about a square yard in extent. The tail was large, and nearly all the bones were solid. The diminutive head will first attract attention, as it is smaller in proportion to the body than in any vertebrate hitherto known. The entire skull is less in diameter or actual weight than the fourth or fifth cervical vertebra. . . . The very small head and brain, and slender neural cord, indicate a stupid, slow-moving reptile. The beast was wholly without offensive or defensive weapons, or dermal armature. In habits, *Brontosaurus* was more or less amphibious, and its food was probably aquatic plants or other succulent vegetation. The remains are usually found in localities where the animals had evidently become mired."

Of still more stupendous bulk is *Atlantosaurus immanis*, the femur of which has the enormous length of six feet two inches, and thus

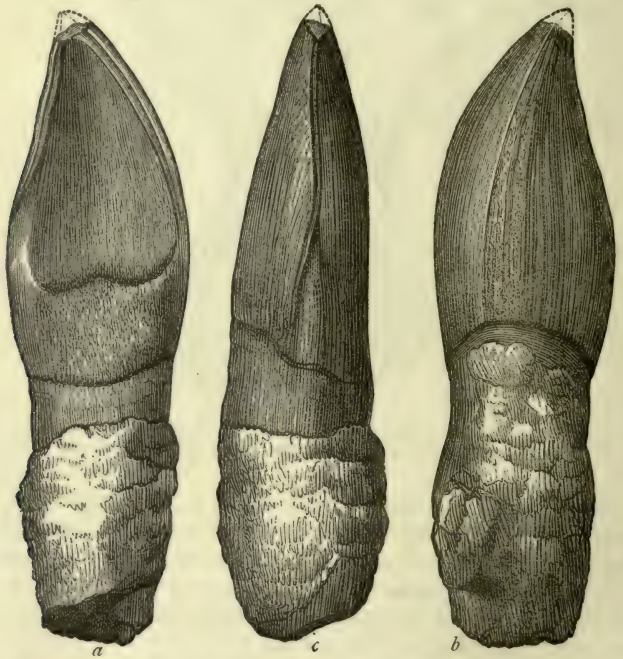

Fig. 1075.—Inner (*a*), outer (*b*), and profile (*c*) views of a tooth of *Hoplosaurus armatus*; from the Wealden of the Isle of Wight. (After Wright.)

indicates one of the largest land animals yet known; the only form which could possibly have exceeded it being the Cretaceous *Triceratops* mentioned above. It is by no means clear that all these

American types are generically distinct from those to be now mentioned.

We may now proceed to the consideration of certain European Dinosaurs which from their more or less close alliance to the preceding forms appear to belong to the same family, although opinions to the contrary have been expressed. It may be observed in this connection that the study of all the European Sauropoda is beset with almost insurmountable difficulties owing to the circumstance that nearly all the specimens are disassociated, and that genera and species have been named on the evidence of single teeth, vertebræ, or bones of the limbs or limb-girdles, so as not to admit of comparison with one another. Moreover, the unwieldy bulk of the specimens themselves is a bar to an exact comparison, even when they are strictly comparable one with another.

The tooth from the Wealden of the Isle of Wight, represented of the natural size in fig. 1075, has been made the type of the genus *Hoplosaurus* (*Oplosaurus*), and it appears almost certain that cervical and dorsal vertebræ, and a pelvis from the same deposits, described under the names of *Ornithopsis Hulkei* and *O. eucamerotus*, are referable to the same form. These remains indicate a Reptile of considerably smaller dimensions than *Brontosaurus*, having a pelvis which approximates in structure to that of *Atlantosaurus*. The ischium, which has the downward direction characteristic of the present family, has a length of 27 inches, and is comparatively wide in proportion to the pubis. The genus *Pelorosaurus* is typified by a huge humerus from the Wealden of Sussex, measuring some 54 inches in length, which would appear far too large for the type species of *Hoplosaurus*.[1] A slightly larger humerus from the Kimeridge Clay, originally described as *Cetiosaurus humerocristatus*, appears generically inseparable from *Pelorosaurus*, and its owner was in all probability very closely allied to an equally large form from the Oxford Clay, described upon the evidence of the pelvis as *Ornithopsis Leedsi*. Of the latter the lumbar and caudal vertebræ are also known, and approximate closely, both in size and contour, to those of *Brontosaurus*, the lumbars having a diameter of nearly 12 inches across the centrum. In the pelvis the ischium measures nearly 36 inches in length, and is also narrower in proportion to the pubis than in *Hoplosaurus*—differences which, coupled with others, may probably be regarded as of generic value. Referring all these forms, at least provisionally, to *Pelorosaurus*, it would appear that this genus includes very large *Dinosaurs* closely allied both in vertebral and pelvic characters, as well as in point of size, to *Brontosaurus*, al-

[1] Compare the proportions of this bone and of the ischium mentioned below with the corresponding dimensions of other Dinosaurs given in the table on the next page.

though it is probable that the humerus was relatively longer. Teeth from the Kimeridgian of Boulogne, upon the evidence of which the genus *Neosodon* was founded, but which were subsequently identified with American forms described as *Caulodon*, are probably referable to the same species. Small vertebræ from the Kimeridge Clay of Swindon, upon which the genus *Bothriospondylus* was established, may perhaps be referable to a very young individual of *Pelorosaurus humerocristatus;* while a comparatively small humerus from the same deposits, originally described under the preoccupied name of *Ischyrosaurus*, may indicate a smaller species of the same genus. Finally, of the Kimeridgian remains described as *Gigantosaurus*, while some may be referable to *P. humerocristatus*, a sacral vertebra may belong to the smaller *P. Manseli* above mentioned.

The following table gives the dimensions of some of the bones of certain of the above-mentioned forms, together with those of others noticed below under the head of the *Cetiosauridæ :—*

	Atlantosaurus.	*Brontosaurus.*	*Pelorosaurus Conybeari.*	*Pelorosaurus humerocristatus and Leedsi.*	*Hoplosaurus.*	*Morosaurus* (type).	*Cetiosaurus.*	*Morosaurus brevis.*
Length of scapula . .	...	60	...	...	...	45	54	...
" humerus . .	...	50?	54	57	...	36	51.5	24
" ischium . .	...	40	...	35.5	27	30.5	39?	...
" femur . .	74	70?	...	...	...	46	64	...
Width of dorsal centrum .	...	13	...	...	8.5	...	...	6
" lumbar " .	...	14	...	11.5[1]	...	...	...	7
" caudal " .	...	12	...	...	...	...	?10	7

Family Diplodocidæ.—The genus *Diplodocus*, from the Upper Jurassic of North America, is typically represented by a species of smaller size than many of the preceding forms, and is regarded by Professor Marsh as the type of a family. It was originally considered that the external nares were single, and situated at the top of the skull between the orbits (fig. 1076); but it now appears that they really formed long narrow slits between the premaxillæ, nasals,

[1] Caudal vertebræ of a larger individual are nearly equal in size to those of *Brontosaurus*.

and maxillæ, after the fashion obtaining in Pterodactyles and Birds. And it is probable that a similar arrangement exists in the other members of the suborder. It will be observed from the figure that the jugal bifurcates posteriorly to form the anterior and inferior borders of the orbit; while the quadratojugal joins the maxilla without the intervention of the jugal, which is thrust up. These peculiar features are repeated, as will be noticed below, in one genus of the Ornithosauria. The pelvis is of the general type of

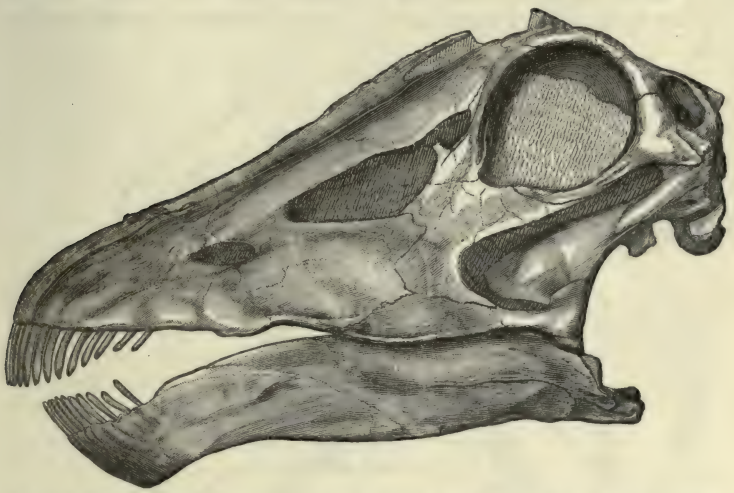

Fig. 1076.—Left lateral aspect of the skull of *Diplodocus longus*; from the Upper Jurassic of North America. One-sixth natural size. The position of the nares at the top of the skull is incorrect. (After Marsh.)

that of the last family; but the distal extremity of the ischium is not expanded.

Family Cetiosauridæ.—This family is typically represented by the English genus *Cetiosaurus*, which, so far as can be determined from the characters of the scapula and pelvis, appears to be so nearly related to the American *Morosaurus* that there seems every reason for including the latter in the same family. *Cetiosaurus* occurs typically in the Lower Jurassic Great Oolite, and Forest-Marble of Oxfordshire and Northamptonshire, where we meet with the huge *C. oxoniensis*. Comparatively small teeth from the same deposits, described under the earlier name of *Cardiodon rugulosus*, are of the same general type as those of *Hoplosaurus*, but have relatively smaller crowns, with a more incurved summit, and are clearly distinct from the last-named genus. Professor Phillips referred teeth of this type to *C. oxoniensis*, but from their small size they

would agree better with a dorsal vertebra from the same deposits subsequently described as *Bothriospondylus robustus*. This vertebra is somewhat longer than the dorsals of *C. oxoniensis*, but need not be generically distinct. In *Cetiosaurus* the caudal vertebræ have no distinct postzygapophyses, and articulate by two facets with the chevrons, of which the upper extremities are not united, as in Crocodiles. The scapula is much expanded at its distal extremity, and the humerus, though long, is wider and shorter than in the European forms mentioned among the *Atlantosauridæ*. The ischium appears to be of the same general type as that of *Morosaurus* (fig.

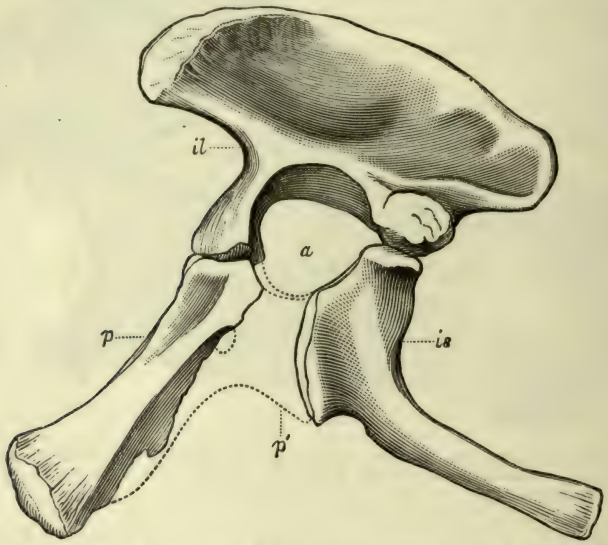

Fig. 1077.—The left side of the pelvis of *Morosaurus grandis*; from the Upper Jurassic of North America. One-sixteenth natural size. *a*, Acetabulum; *il*, Ilium; *is*, Ischium; *p*, *p'*, Pubis. (After Marsh.)

1077), in which the shaft is bent backwards and has no distal expansion, while the symphysis does not extend to the extremity; thus causing the middle of the acetabular part to be far above the axis of the shaft.

The typical species of *Cetiosaurus* is comparatively well known through the labours of the late Professor Phillips. This huge reptile was perhaps somewhat smaller than *Pelorosaurus*; and it was inferred from the well-ossified extremities of the limb-bones, the free projection of the head of the femur into the acetabulum, and the large terminal claws, that this creature was of terrestrial or subaquatic habits, and that it probably dwelt on the banks of lakes or rivers among brakes of ferns, cycads, and conifers. From the structure of a tooth (*Cardiodon*) found in the same

beds, the Cetiosaur was inferred to have been of herbivorous habits. How remarkably these conclusions have been confirmed by the discovery of the allied American forms, is now a matter of history.

In the Wealden sacral and caudal vertebræ of the general type of those of *Cetiosaurus*, described under the name of *Cetiosaurus brevis*, indicate a smaller form than *Hoplosaurus*. It is probable that a dorsal vertebra from the same deposits, described as *Bothriospondylus elongatus*, as well as a humerus and other bones of the pectoral limb, to which the name *Morosaurus Becklesi* has been applied, are referable to the same form, which would appear to be generically distinct from *Cetiosaurus*, and may be known as *Morosaurus brevis*. The dimensions of some of the bones are given in the table on p. 1176. An ilium, from the same beds, closely resembles that of the American genus, and probably belongs to the same form. In North America, *Morosaurus* and the small *Pleurocœlus* are characteristic of the Upper Jurassic. The dorsal vertebræ of the latter are relatively elongated, and do not exceed five inches in length; those of one species being remarkable for their very low neural arches. Small teeth from the Wealden (fig. 1078), once referred to *Hylæosaurus*, probably belong to a species of *Pleurocœlus*. These teeth are less spoon-shaped, and approximate more to a compressed cone than those of *Morosaurus* (fig. 1072); and the genus *Pleurocœlus* includes the smallest representatives of the suborder. The pelvis of *Morosaurus* is shown in fig. 1077; the teeth (fig. 1072), although considerably larger than those of *Cardiodon* and *Pleurocœlus*, exhibit the same incurving of the crown.

Fig. 1078. — Outer and profile views of a tooth of *Pleurocœlus valdensis*; from the Wealden.

In the preceding forms the centra of the caudal vertebræ are amphicœlous; but *Titanosaurus*, originally described from the Cretaceous of India, and subsequently found in the English Wealden and Upper Greensand, has procœlous centra to these vertebræ. The femur of this genus indicates an animal as large as *Cetiosaurus*.

Remains of other Cretaceous Sauropoda have received distinct generic names, but some of them may be identical with the above-mentioned types. Thus we have *Dinodocus* based on broken bones from the Lower Greensand of Kent; and *Æpysaurus* founded on a humerus from the French Cretaceous. *Macrurosaurus*, from the Cambridge Greensand, is a smaller form, with imperfectly procœlous caudal vertebræ. Finally, the name *Thecospondylus* has been applied to a specimen from the Wealden, of which even the subordinal position cannot be determined, although it has been suggested,

without sufficient foundation, that it indicates a form allied to *Cœlurus*.

Order IX. Crocodilia.—The Crocodiles of the present day are well-known, lacertiform Reptiles inhabiting the lakes, rivers, and marshes of the warmer regions of the globe; and are the largest existing representatives of the entire class. If we had only these existing and specialised forms to deal with, we should have no difficulty in giving a concise definition which would separate the order to which they belong from the Dinosauria. There occur, however, in the Trias a number of generalised forms which approximate so closely to the latter order as to render such definition extremely difficult; and it is quite possible that some of the undermentioned characters are not applicable to the first suborder. The order is sometimes known as the Emydosauria.

In all the forms the limbs and body (fig. 1079) are of a lacertiform type, the former being very short, and the latter long and

Fig. 1079.—Head and fore-part of the body (A) and hind foot (B) of *Crocodilus porosus*; from Madras. Much reduced. (After Günther.)

carried close to the ground; while the tail is relatively long. With the exception of a few later Jurassic forms, the dorsal aspect of the body carries a dermal armour of articulating or imbricating bony scutes, arranged in two or more longitudinal rows (fig. 1079), and marked on their outer surface by a series of deep pits. In certain cases there may also be an armour of similar type developed on the ventral surface of the body. The centra of the vertebræ are either amphi- or procœlous, and the neuro-central suture is persistent.

The cervical vertebræ have double pedunculate costal tubercles, situated one on the centrum and the other on the arch; and the cervical ribs have long processes projecting anteriorly and posteriorly, which completely prevent the head from being turned sideways. In the dorsal region usually the four anterior vertebræ have the transverse process for the articulation of the tubercle of the rib placed on the arch, while there is a lower process, or rib-facet, on the centrum for the capitulum of the rib; but posteriorly this rib-facet rises on to the arch, and in the middle dorsals forms a kind of "step" on the transverse process, while still more posteriorly it merges with the tubercular facet. The dorsal ribs have uncinate processes, like those of Birds; and the chevron-bones of the caudal region usually have the upper limbs of the Y not united

Fig. 1080.—Oblique left lateral and superior view of the skull of *Crocodilus palustris*; India. Much reduced. The small paired apertures to the right are the supratemporal fossæ, in advance of which are the orbits communicating posteriorly with the infratemporal fossæ.

by bone. Normally the sacrum has but two vertebræ.[1] The skull (fig. 1080) is relatively large in proportion to the body, and is usually much depressed; its component bones are firmly united, and generally have a characteristic sculpture on their external surface. The palatines and pterygoids unite in the middle line, and thus close the palate; and very frequently one or both of these paired bones develop inferior plates, which meet beneath the narial passages (fig. 1089). The quadrate is tightly wedged in among the adjacent bones; the tympanic cavities usually communicate with the mouth by three eustachian canals; the mandibular symphysis unites by suture; and there are generally no ossifications in the sclerotic of the eyeball. There is almost invariably a lateral vacuity in the mandible (fig. 1093). The teeth are always either pointed

[1] As an abnormality three sacrals may be present.

and subconical, or laterally compressed. In the sternal region the sternum itself is cartilaginous; and there is a bony interclavicle, but generally no clavicle. In the pelvis (fig. 1081) the ilium is short and deep, without distinct preacetabular or pubic processes; the ischium is stout, and devoid of obturator process; while the pubis[1] is directed downwards and forwards, and is frequently excluded from the acetabulum. In regard to the pectoral girdle and limbs, it will suffice to say that all the bones are solid; that the coracoid has a fontanelle, and may be either short or long; that in the humerus and femur the heads are imperfectly differentiated, that of the latter being compressed and placed very obliquely to the plane of the condyles; while the shaft of the femur has no inner trochanter. Moreover, the tibia has no cnemial crest at its proximal extremity. The habits of all the members of the order are quadrupedal; and the feet (fig. 1079) are plantigrade, those of the hind limbs being partially webbed.

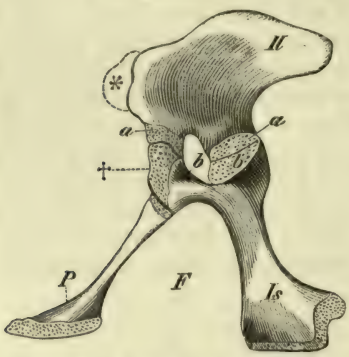

Fig. 1081.—Left side of the pelvis of a young *Alligator*. *Il*, Ilium; *Is*, Ischium; *P*, Pubis; *a*, *b*, *b*, Acetabulum, with its vacuity; *F*, Obturator notch; †, *, Cartilaginous processes of the ischium and ilium.

The existing Crocodiles present many peculiarities in regard to the soft parts; but since we do not know whether the same features occurred in the generalised fossil forms, and cannot compare them with extinct orders, it is unnecessary to allude to them further.

This order is peculiarly interesting, not only as containing the on y existing members of the Archosaurian branch; but also since it affords a beautiful example of the gradual evolution of specialised characters as we ascend in the geological scale.

Suborder 1. Aëtosauria.—This provisional suborder includes but a single family, which Dr Baur places in the Crocodilia, although Professor Cope regards it as more nearly related to the Rhynchocephalia, to which it perhaps belongs.

Family Aëtosauridæ.—This family is typically represented by the genus *Aëtosaurus*, of the Upper Trias of Würtemberg; a small form with Crocodilian armour and limbs, but with the metatarsals much elongated, and approaching in many points of its organisation to the Theropodous Dinosauria, to which Professor Marsh regards

[1] It has been suggested that the bone termed pubis in the Eusuchia is really a prepubis.

it as nearly related. *Typothorax*, with pitted scutes adherent to the ribs, is an allied form from the reputed Trias of North America; which Professor Cope regards as foreshadowing in its dermal skeleton the carapace of the Chelonia.

Suborder 2. Parasuchia.—This extremely generalised suborder is confined to the Trias, or strata of approximately equivalent age. It is characterised by the absence of descending palatal plates developed from the roof of the mouth, so that the posterior nares (fig. 1083) open directly into the latter, without the intervention of a secondary passage. The vomers are seen on the palate; the middle one of the three eustachian canals appears to be wanting[1]; the anterior nares are placed in the middle of the cranium; and the premaxillæ have typically some twenty-one teeth, and are produced into a long rostrum. A clavicle was probably present, the coracoid was short and rounded like that of the Dinosauria; while the pubis, as in the latter, takes a share in the formation of the acetabulum; and each foot was probably furnished with five digits. The centra of the vertebræ are amphicœlous; and the dorsal scutes have a keel-like ridge, and form only two longitudinal rows; while those of the ventral buckler (when present) are arranged in not more than eight of such rows, and each scute consists of a single bone. This group differs very widely from the true Crocodiles, and Dr Baur now appears to regard it as a distinct order, under the name of Phytosauria.

Family Phytosauridæ.—This family is best known by the type genus *Phytosaurus* (*Belodon*); originally described from the Keuper,

Fig. 1082.—Right lateral view of the skull of *Phytosaurus cylindricodon;* from the Keuper of Würtemberg. Much reduced. The vacuities in the cranium are the preorbital, the orbit, and the infratemporal fossa. (After Meyer.)

or Upper Trias of Würtemberg, but subsequently found in beds of approximately equivalent age in both India and North America. In the skull (figs. 1082, 1083) the orbit is separated by a bony bar from the infratemporal fossa; there is a large preorbital vacuity,

[1] According to Dr Koken.

and the supratemporal fossa is exceedingly small. The nasals reached the premaxillæ and completely surrounded the nares—thus presenting a feature unknown in any other vertebrate; while the orbits were somewhat irregular in contour, and directed in part laterally, and in part frontally. The teeth are sharp and pointed,

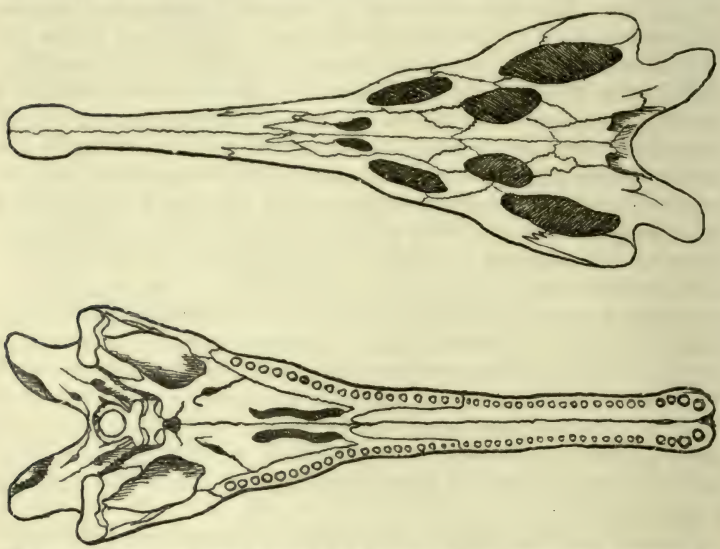

Fig. 1083.—Frontal and palatal aspects of the cranium of *Phytosaurus cylindricodon*. The anterior vacuities in the upper figure are the anterior nares, and the slits in the lower figure are the posterior nares. (After Meyer.)

with serrated antero-posterior ridges (carinæ); and in the anterior part of the jaw (fig. 1084) are subcircular in transverse section, but posteriorly are laterally compressed. There was no ventral armour. In the apparently nearly allied *Stagonolepis*, of the Upper Trias (Keuper) of Elginshire, there was, however, a well-developed ventral dermal armour; the teeth were blunt and swollen; and the pattern of the sculpture on the dorsal scutes was different. This genus was originally founded upon the evidence of these scutes, which were thought to have belonged to a Ganoid Fish. The name *Episcoposaurus* has been applied to a North American Triassic form which is regarded by Professor Cope as allied to *Phytosaurus*.

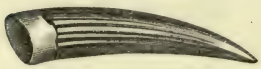

Fig. 1084.—Tooth of *Phytosaurus carolinensis*; from the Trias of South Carolina. Reduced.

Family Parasuchidæ.—The single genus *Parasuchus* occurs in the same lower Mesozoic horizon (Maleri beds) in India which

yields the remains of *Phytosaurus*, and is very imperfectly known. It differs from the preceding family by the structure of the ventral part of the basioccipital, which approximates to the Rhynchocephalian type.

Suborder 3. Eusuchia.—This suborder is taken to comprise all the post-Triassic Crocodilia. These were, indeed, originally divided into two suborders, but subsequent researches have shown that they are so closely connected as to render such division inadvisable. In all these forms the premaxillæ, maxillæ, and palatines develop inferior palatal plates meeting in the middle line beneath the narial passage, and thus completely separating the latter from the mouth, and causing the formation of secondary posterior nares, which in some instances are situated immediately behind the palatines, but in others (as in the figure of *Crocodilus* given on page 1192), owing to the development of similar plates by the pterygoids, behind the latter bones. The object of this peculiar arrangement is to enable these animals to drown their prey by holding it in their open mouths under water, which is thus entirely prevented from entering the air passages. A gradual evolution of this structural feature can be traced from the last suborder, where it is entirely wanting, to the generalised, and thence to the most specialised, members of this division. Other characteristic features are found in the terminally-situated, and usually undivided, nares; in the non-appearance of the vomers on the palate; in the bony middle eustachian canal; and the presence of not more than four or five teeth in the premaxillæ. There is no clavicle; the coracoid is much elongated; the pubis is entirely excluded from the acetabulum (fig. 1081); and there are five digits in the manus and four in the pes (fig. 1079). This suborder may be divided into two series according to the development or non-development of palatal plates by the pterygoids, and the form of the vertebræ.

The occurrence in all the groups of the Eusuchia of long-jawed and short-jawed forms is so suggestive of the direct origin of the existing Gharials from long-jawed Mesozoic types, and of the Crocodiles and Alligators from short-jawed forms of the same epoch, that Dr Koken adopts this view, and divides the families according to this grouping. There is, however, considerable difficulty in accepting this view, since it would appear unlikely that all the modern Crocodilians would have attained such a similarity in cranial and vertebral characters if they had totally different origins.

A. Amphicœlian Series.—In this the more generalised series the centra of the vertebræ are usually amphicœlous; the pterygoids do not develop palatal plates; and the dorsal scutes are usually arranged in only two longitudinal rows, and are keel-less. The ventral buckler is generally divided into an anterior and a posterior

portion, but may be single; while in the transverse rows of this buckler the scutes always imbricate anteriorly, but in the posterior part usually articulate by suture; each scute being invariably composed of a single piece of bone.

It may be incidentally mentioned here that while in the anterior region of the ventral buckler of all Crocodiles the component scutes of each transverse row articulate together by suture with those on either side, yet, as will be gathered from the foregoing characters, in the posterior portion of the same buckler in the present series the articulation of the different transverse rows with one another may be either by suture, or by imbricating like the tiles on a roof.

The present series ranges in time from the Lias to the Lower and Middle Cretaceous, and is especially characteristic of the European strata.

Family Teleosauridæ.—The members of this family are readily distinguished from the more specialised forms by the circumstance that the supratemporal fossæ are always much superior in size to the orbits, and that the latter are completely separated by a bony bar from the infratemporal fossæ; both these features being well shown in the accompanying figure of the cranium of *Steneosaurus*. In front of the orbit there is always a well-marked vacuity (not

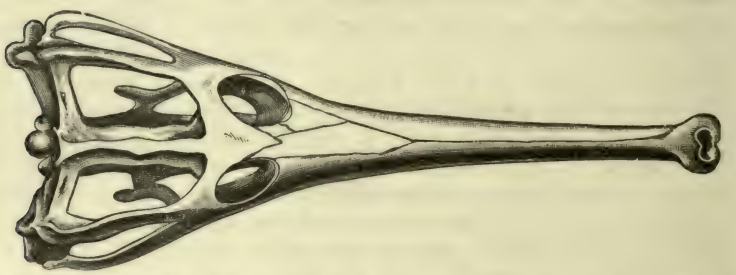

Fig. 1085.—Upper view of the cranium of *Steneosaurus Heberti*; from the Oxford Clay of France. Much reduced. The bones on the right side of the rostrum are imperfect, and there should have been a line connecting the apex of the frontals with the suture dividing the maxillæ. The large vacuities behind the orbits are the supratemporal fossæ, below which are the infratemporal fossæ.

shown in the figure); the dorsal scutes, when present, are rounded, and arranged in two longitudinal rows; while the ventral buckler is divided, and the component scutes of the posterior transverse rows are united by suture. The axis vertebra carries two facets for its rib, as in Dinosaurs. The members of this family were of marine habits, and range throughout the Lias and Jurassic system of Europe. They may be divided into two subfamilies.

In the subfamily *Teleosaurinæ* the skull is generally produced into a long slender rostrum, like that of the existing Gharial; the nasals

are separated by a long interval from the premaxillæ; the orbits are of regular contour, and directed more or less completely frontally; while the nares look more or less anteriorly. The dermal armour is fully developed, and sclerotic plates were not present in the eye. The type genus *Teleosaurus* comprises small or medium-sized species, and is readily characterised by the teeth being inclined horizontally outwards, and extremely numerous. It is confined to the Lower Jurassic, and is abundant in the Stonesfield slate of Oxfordshire, and the nearly equivalent beds of Caen, in Normandy. The most abundant genus is, however, *Steneosaurus* (fig. 1085), in which *Mystriosaurus* may be included, characterised by the elongated snout, the nearly vertical direction of the teeth, and the large size of the supratemporal fossæ, which in some species attain enormous dimensions. In the Liassic forms, separated generically by some writers as *Mystriosaurus*, the orbits are somewhat oblique, and the supratemporal fossæ are never excessively large; but in the numerous species of the Lower and Middle (Oxford Clay) Jurassic the direction of the orbits is entirely frontal, and the supratemporal fossæ are very large. In the figured *S. Heberti*, of the Lower part of the Oxford Clay, the skull is somewhat intermediate in these respects; the orbits being slightly oblique, and the supratemporal fossæ large. This genus does not appear to have survived above the Kimeridge Clay. In *Pelagosaurus* (fig. 1086) we have an

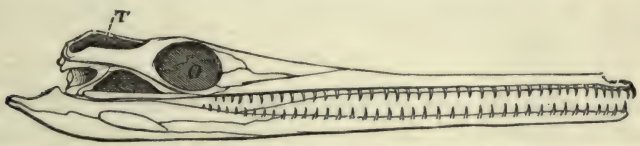

Fig. 1086.—Right lateral view of the skull of *Pelagosaurus typus*; from the Upper Lias of Normandy. Reduced. *T*, Supratemporal fossa; *O*, Orbit.

allied genus, represented only by two species of Liassic age; it is distinguished from the preceding by several characters; but more especially the form of the posterior nares, and the smaller and rounded supratemporal fossæ. The remains of the small *P. typus* are especially abundant in the Upper white Lias of Normandy, and the marvellously perfect preservation of some of the skeletons has enabled the bony anatomy of this species to be as completely studied as in the case of an existing form. In *Machimosaurus*, of the Kimeridge Clay (Upper Jurassic) of both England and the Continent, and *Teleidosaurus*, of the Fullers' Earth (Lower Jurassic) of Normandy, we have two genera in which the skull becomes much shorter and broader, the teeth stouter and less numerous, and the orbits more oblique; and which thus connect the present with the

next subfamily. *Machimosaurus*, which occurs both in France and England, is the largest member of the order, the length of the mandible exceeding 50 inches; the skull has been referred to *Pliosaurus*. The teeth closely resemble those of *Goniopholis*, having conical and deeply fluted crowns.

With the second subfamily, or *Metriorhynchinæ*, we come to a very remarkable group of Crocodiles, presenting certain specialised features unknown elsewhere in the entire order. The skull (fig. 1087) is either of moderate length or comparatively short; the nasals are either in contact with the premaxillæ, or separated therefrom by a short interval; the nares are directed frontally; the orbits are of very irregular contour, and placed completely on the sides of the skull; and the teeth, which are never very numerous, are always of considerable size, and directed more or less nearly

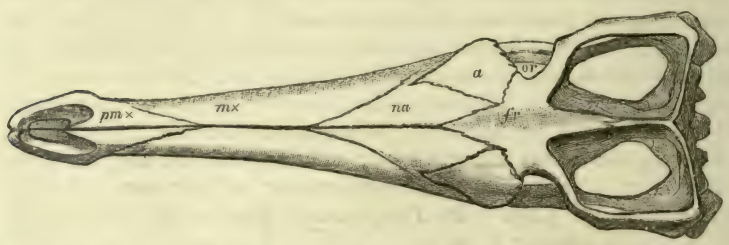

Fig. 1087.—The cranium of *Metriorhynchus hastifer*; from the Kimeridge Clay of Normandy. One-sixth natural size. *pmx*, Premaxilla; *mx*, Maxilla; *na*, Nasal; *a*, Prefrontal; *fr*, Frontal; *or*, Orbit. (After Deslongchamps.)

vertically, while there is no vacuity in the mandible. The most remarkable features of the group are, however, the development of a ring of bony plates in the sclerotic of the eye, and the general or universal absence of a dermal armour. It is, indeed, very curious to notice the correlation of these two features, since there is no known instance of the presence of both sclerotic plates and of dermal scutes in any reptile. The pelvis of this subfamily is also worthy of notice. Thus the ilia are very small subtriangular bones articulating with long and downwardly curved sacral ribs; while the ischia are enormously large, with the shape of an isosceles triangle. This presents a remarkable contrast to *Steneosaurus*, where the sacral ribs are straight and directed outwards, while the ilium is larger, with a considerable portion projecting above the costal articulation. In the genus *Metriorhynchus* the skull (fig. 1087) is of moderate length, and frequently somewhat slender, with the frontal region slightly sculptured; there is a more or less well-marked premaxillary expansion; the prefrontals (*a*) are very large, and overhang the orbits; while the teeth are curved and carinated, with the

enamel generally fluted at the base of the crown, but without serrations on the carinæ. The pectoral limbs are extremely small. This genus ranges from the Oxford Clay to the Portland Oolite.

In the Oxford Clay and Kelloway rock, both of the Continent and England, we meet with *M. superciliosus* and *M. moreli*, which are readily distinguished by the sculpturing of the frontals and the form and relations of the prefrontals. Beautiful examples of this genus occur in the Oxford Clay near Peterborough, which exhibit the absence of dermal scutes; a skull from this locality, to which the name *Steneosaurus dasycephalus* has been applied, may be referred to *M. superciliosus*. The Portlandian form was described as *Steneosaurus gracilis*. It is probable that *Gnathosaurus* and *Rhacheosaurus* are synonyms. The most specialised genus is *Geosaurus* (*Cricosaurus* or *Dacosaurus*), in which the skull is comparatively short, and is devoid of frontal sculpture, and also of the premaxillary expansion; while the teeth (fig. 1088) are compressed, smooth, and carinated, with distinct serrations on the carinæ. The type species, which occurs in the Lower Kimeridgian of Bavaria,

Fig. 1088.—Crown of tooth of *Geosaurus maximus*; from the Kimeridge Clay of Ely. (After Wood-Mason.)

and is of comparatively small size, was long thought to belong to the *Mosasauridæ*. A much larger form, occurring in the Kimeridge, and perhaps the Oxford, Clay of England and the corresponding beds of the Continent, has been described under the name of *Dacosaurus*, but can be only specifically distinguished from the type. A tooth is shown in the accompanying woodcut. It is not improbable that vertebræ from the Lower Greensand of Germany, described under the name of *Enaliosuchus*, indicate a closely allied form.

As members of this family, of which the serial position is uncertain, may be mentioned small forms respectively from the Kimeridgian of Bavaria and France, to which the names *Æolodon* and *Crocodilæmus* have been applied, both of which have a dermal armour; the ventral shield consisting of a number of small and closely-joined scutes. In the type of *Æolodon* these scutes are only slightly pitted, and the teeth alternate in size.

Family Goniopholididæ.—The members of this family resemble

existing Crocodiles in having an open channel connecting the infratemporal fossa with the orbit. The orbits themselves are, moreover, usually but slightly smaller than the supratemporal fossæ, or only exceed them but little in size; while there is no preorbital vacuity. The dorsal scutes are rectangular, and may be arranged either in two or in several longitudinal rows; while the ventral armour may form either a single or a double buckler, in which the posterior transverse rows of scutes may either imbricate or articulate by suture. The members of this family inhabited freshwaters, and they range in time from the Purbeck (Upper Jurassic) to the Wealden (Lower Cretaceous), and not improbably also to the Upper Greensand. Nearly all the known forms are European, but one genus which may belong to this family is American; and the family is probably also represented in the Cretaceous of India. Three subfamily divisions have been proposed, but before discussing these we may allude to the genera *Suchosaurus* of the English Wealden, and *Hyposaurus* of the Cretaceous of North America and Brazil, which not improbably belong to this family, although their precise affinities are not yet satisfactorily determined. The type of the former genus is of very large size, and has the teeth greatly compressed; while in the latter the posterior teeth are of this type, but the anterior ones are rounded like those of *Goniopholis*, and the symphysis of the mandible is elongated.

The first subfamily, or *Petrosuchinæ*, is very imperfectly known, and is represented only by the genus *Petrosuchus*, of the English Purbeck beds, in which the posterior nares are placed near the middle of the skull, as in many of the *Teleosauridæ*, and the orbits are considerably smaller than the supratemporal fossæ. The cranium itself is of moderate length.

The members of the second subfamily, or *Goniopholidinæ*, have the posterior nares placed more posteriorly than in the preceding group; while there are two longitudinal rows of dorsal scutes; and the ventral buckler is divided, with the transverse rows of scutes in the posterior portion articulating by suture. In the first, or Longirostrine, section of this subfamily the skull is elongated like that of the existing Gharial; the nasals do not reach the nares, the splenial bone enters into the mandibular symphysis, and the teeth are numerous, and all nearly similar in size. It is represented only by *Pholidosaurus* (*Macrorhynchus*) of the German and English Wealden. In the Brevirostrine section, on the other hand, the skull is short, like that of the true Crocodiles, the nasals sometimes reach the nares, the splenial enters but very slightly into the symphysis of the mandible, and some of the teeth are much larger than the others. The dorsal scutes present the peculiarity of articulating with one another by means of a peg at one angle which fits into a

socket in the adjacent scute; an arrangement very similar to that obtaining in the scales of certain Ganoid fishes. The genus *Goniopholis* is very characteristic of the Wealden and Purbeck, and has a cranium of moderate length, with the nasals not reaching the nares, and the orbits rather smaller than the supratemporal fossæ. The type species attained very large dimensions, and was long since made known to the world by the late Dr Mantell, under the name of the Swanage Crocodile; its blunt and grooved teeth, and characteristic scutes, being comparatively common in the Wealden stone quarries of Sussex. This genus has been recently recorded from the Jurassic of North America, where it had been previously described as *Amphicotylus*. Allied but considerably smaller forms from the Dorsetshire Purbeck constitute the genera *Nannosuchus* and *Oweniasuchus* (*Brachydectes*). The most specialised genus, however, appears to be the minute *Theriosuchus* of the Purbeck, which, in having the orbits slightly larger than the supratemporal fossæ, approximates to the next subfamily, although retaining the pegged dorsal scutes of *Goniopholis*. The nasals in this genus reach and partly divide the nares, as in the true Crocodiles; and we thus have a comparatively close approximation to existing forms, which is rendered still more manifest by the members of the next group.

In the genus *Bernissartia*, of the Belgian Wealden, which forms the type of the subfamily *Bernissartiinæ*, the skull is comparatively short and broad, and has the posterior nares placed very close to the occipital condyle; while the orbits are decidedly larger than the supratemporal fossæ. Like existing Crocodiles, these reptiles were provided with more than two longitudinal rows of dorsal scutes (which have no peg-and-socket); while their ventral buckler is undivided, and has the transverse rows of scutes imbricating throughout. The resemblance to existing forms being completed by the pectoral limbs being considerably shorter than the pelvic pair. The vertebræ, however, still retained the primitive amphicœlous character. It seems probable, from the position of the posterior nares, that the imperfectly known genus *Hylæochampsa*, from the English Wealden, is a closely allied form of rather larger dimensions; and it is not unlikely that certain procœlous vertebræ from the same formation which have been described under the name of *Heterosuchus* may belong to this form; while others from the Cambridge Greensand and the Greensand of Austria, which have been referred to *Crocodilus*, may also indicate allied reptiles, although there is a possibility that the owners of these vertebræ belonged to the next series. It will thus be seen that if *Hylæochampsa*, or an allied form, had such procœlous vertebræ, it would only require the development of palatal plates to the pterygoids to convert it into a Crocodilian of the modern type; and it is highly probable that such a form once ex-

isted, since it is most unlikely that the change from amphicœlous to procœlous vertebræ took place precisely at the same time as the pterygoids developed palatal plates. On the other hand there is an equal *primâ facie* probability that these two changes may have occurred in the reverse order to that indicated above.

B. Procœlian Series.—In this series the vertebræ, with the exception of five, are procœlous; the pterygoids develop palatal plates to prolong the narial passage (fig. 1089); and all the eustachian canals are enclosed in bone. The dorsal scutes are, moreover, always arranged in more than two longitudinal rows; and when there is a ventral buckler it is undivided, and invariably consists of more than eight rows of imbricating scutes, in which each scute is composed of two separate pieces of bone. The axis vertebra differs from that of the *Teleosauridæ*, in having no costal articulations; its rib having been shifted forward on to the centrum of the atlas, or odontoid process.

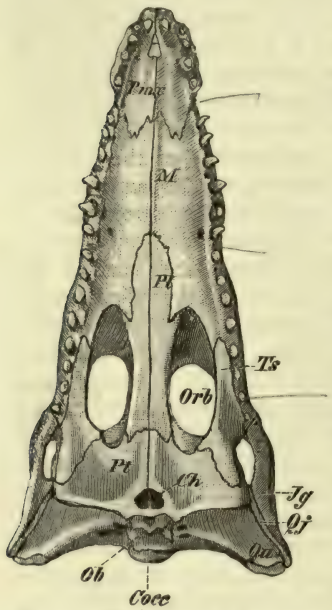

Fig. 1089.—Palatal aspect of the cranium of *Crocodilus*. Reduced. *Pmx*, Premaxilla; *M*, maxilla; *Pl*, Palatine; *Ts*, Transverse; *Pt*, Pterygoid; *Jg*, Jugal; *Qj*, Quadratojugal; *Qu*, Quadrate; *Ob*, Basioccipital; *Cocc*, Occipital condyle; *Orb*, Orbit; *Ch*, Posterior nares.

Family Crocodilidæ.—All the sufficiently known members of this series may be included in a single family, which agrees with the *Goniopholididæ* in the free communication of the infratemporal fossa with the orbit, which is considerably larger than the supratemporal fossæ. This family is first definitely known from the Upper Cretaceous, and continues to the present day, being represented in the freshwaters of most of the warmer regions of the globe. If, however, the procœlous vertebræ mentioned in the last series from the Greensand and Wealden really indicate members of the present family, it will date from the latter horizon. The form of the skull affords grounds for two sectional divisions.

The Longirostrine section is represented at the present day only by the true Gharial (*Garialis*) of the Ganges, and Schlegel's Gharial of Borneo. The skull is produced into a long narrow rostrum (fig. 1091), with the dental borders nearly straight; the nasals never extend to the anterior nares, and are frequently separated from the

premaxillæ; the supratemporal fossæ are of somewhat large size, and sometimes exceed the orbits in this respect; while the mandibular symphysis is very long, and embraces the anterior portion of the splenial bone. The teeth are always numerous, and are only slightly unequal in size; and neither of the existing species is provided with a ventral armour. In this group *Rhamphosuchus*, of the Pliocene of the Siwalik Hills of India, was a gigantic form probably between fifty and sixty feet in length, and characterised by the stoutness of the teeth, of which the upper series bites on the outer side of the lower, as in the Alligators, instead of interlocking with them as in other members of this group. In *Thoracosaurus*, again, of the Cretaceous of North America, we have a genus remarkable for retaining the preorbital vacuity of the *Teleosauridæ*, and in having the supratemporal fossa larger than the orbit; both these features apparently pointing to the direct descent of this genus from the last-named family, without having passed through the intermediate stage of the *Goniopholididæ*. The existing Indian *Garialis gangeticus*, of which the dental succession is shown in fig. 1090, is one of the existing species of Reptiles of which remains are found in the Pliocene of the Siwalik Hills. The same deposits have also yielded two more or less nearly allied extinct species; while in the somewhat older beds of Sind there occur two other species differing considerably in the form of the orbit and other cranial characters from the existing representative of the genus. One of these extinct species (*G. pachyrhynchus*) appears to have attained dimensions fully equal to those of *Rhamphosuchus*. Another Gharialoid provisionally referred to the present genus occurs in the Middle Eocene of Bracklesham, in Sussex; while species from the Cretaceous of North America, which have been described under the generic name of *Holops*, may prove to be allied either to the present or to the next genus. In *Tomistoma*, typically represented by the existing *T. Schlegeli* of Borneo, may be included the fossil forms described under the names of *Melitosaurus* and *Garialosuchus* (fig. 1091). This genus is readily distinguished from *Garialis* by the circumstance that the nasals extend forwards to articulate with the premaxillæ (fig. 1091), instead of being separated from them by a long interval. A large fossil form (*Melitosaurus*) occurs in the Miocene of Malta, and a smaller (*Garialosuchus*) in that of Austria. Another Gharialoid,

Fig. 1090. — Teeth of *Garialis gangeticus*, showing succession of germs (*b*, *c*) beneath the tooth in use (*a*). (After Owen.)

from the Upper Cretaceous of France and Maastricht, originally described as *Garialis macrorhynchus*, has also been provisionally included in the same genus. This form is, however, referred by

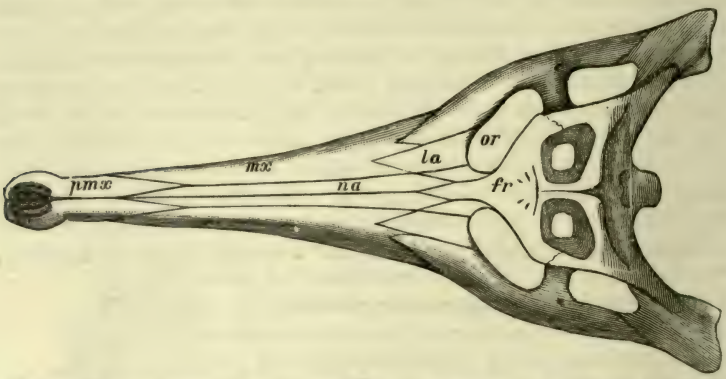

Fig. 1091.—Frontal aspect of the cranium of *Tomistoma eggenburgense*; from the Miocene of Austria. One-tenth natural size. *pmx*, Premaxilla; *mx*, Maxilla; *na*, Nasal; *la*, Lachrymal; *fr*, Frontal; *or*, Orbit. The vacuity behind the orbit is the infratemporal fossa. (After Toula and Kail.)

Dr Koken to *Thoracosaurus*, although it has no preorbital vacuity, and the nasals reach the premaxillæ. It appears to connect the typical *Thoracosaurus* with the existing *Tomistoma*. Finally, the

Fig. 1092.—Oblique left lateral and superior view of skull of *Crocodilus palustris*; India. Much reduced. The two small vacuities to the right are the supratemporal fossæ; those in advance are the orbits, while the single vacuity to the left is the nares; the bones in advance of the latter are the premaxillæ, and those behind the nasals.

imperfectly known *Thecachampsa*, from the Miocene of North America, should probably be placed in the present group.

The second, or Brevirostrine section, includes the true Crocodiles and Alligators, and is characterised by having the skull short, or

moderately elongated, with its dental borders thrown into distinct festoons (fig. 1092); by the nasals always reaching the premaxillæ, and frequently extending down to the anterior nares (as in fig. 1092); and also by the orbits being always larger than the supratemporal fossæ. The short symphysis of the mandible, from which the splenial element is entirely excluded (fig. 1093), is another striking feature. The teeth, moreover, vary in size in different parts of the jaws; and usually the third and ninth in the upper, and the fourth, and frequently also the first and eleventh, in the lower jaw (fig.

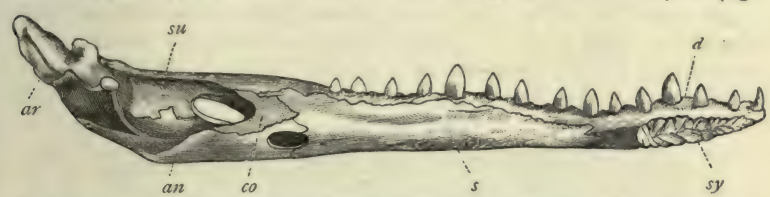

Fig. 1093.—Inner view of the left ramus of the mandible of a Crocodile. Reduced. *an*, Angular; *ar*, Articular; *co*, Coronoid; *d*, Dentary; *s*, splenial; *su*, Surangular; *sy*, Symphysis.

1093), are considerably larger than any of the rest. In the type genus *Crocodilus* the upper and lower teeth mutually interlock; the first lower tooth bites into a perforation or a pit in the cranium, and the fourth into a lateral notch; while the third lower tooth is small. There is, moreover, no ventral armour. This genus is now distributed over nearly all the warmer regions of the globe, and it appears to have had an equally extensive distribution in Tertiary times.

The earliest representative of this genus seems to be *C. Spenceri*, of the Lower Eocene of both England and Italy, which was a species with a comparatively long muzzle like that of the living American *C. intermedius*. The genus is also represented in the Middle Tertiaries of Europe and North America. In the Pleistocene of Queensland we meet with remains of the existing *C. porosus* (fig. 1079), which now ranges from Australia to Eastern India; while in the Pliocene of the Siwalik Hills of India there occur species closely allied to the short-snouted *C. palustris* (fig. 1092) of that country, which makes the nearest approach in cranial characters to the Alligators and their allies.

Diplocynodon is an extinct genus found in the Tertiaries of both Europe and North America, which presents characters intermediate between *Crocodilus* and *Alligator*. Thus the cranium (fig. 1094) is very short and broad; the upper teeth bite on the outer side of the lower; the fourth lower tooth is normally received into a notch (but occasionally into a pit) in the cranium; the third lower tooth is as large as the fourth; and there is a complete ventral armour. In Europe this genus ranges from the Upper Eocene to the Lower Miocene (Upper Oligocene), and is common in the Tertiaries of the

south of England, and also in those of France and Germany; some of the species from the latter deposits having been described as *Alligator*. The genus has also been recorded from the Upper Eocene of North America. The last, and in respect of cranial characters the most specialised, group of Crocodiles is now divided[1] into the two genera *Caiman* and *Alligator*. In these forms both the first and the fourth lower tooth are received into pits in the upper jaw, so as to be concealed when the mouth is closed; the upper teeth bite on the outer side of the lower ones; the supratemporal fossæ are very small, and are occasionally obliterated; and the third lower tooth is smaller than the fourth. *Caiman* is distinguished by the presence of a ventral armour, and also by the circumstance that the nasals do not extend across the nares; and

Fig. 1094.—Oblique left lateral and palatal view of the facial part of the cranium of *Diplocynodon hantoniensis*; from the Upper Eocene of Hampshire. Reduced.

is now confined to Central and South America. In *Alligator*, on the other hand, which occurs at the present day in North America and China, the ventral armour is absent or extremely thin, and the nasals extend forwards so as to divide the narial aperture. Remains which are probably referable to *Caiman* occur in the Pleistocene cave-deposits of Brazil; but it does not appear that there is any certain evidence of fossil species of *Alligator*; the European, and probably some of the North American forms which have been referred to that genus, belonging to *Diplocynodon*. Finally, the name *Isselosaurus* has been recently applied to Crocodilian remains from the Middle Eocene of France which may really belong to one of the above-mentioned genera.

Order X. Ornithosauria.—The Pterodactyles, as the members of this extinct order are commonly termed, are among the most remarkable and strange Reptilian forms that Palæontology has

[1] According to the arrangement adopted by Mr Boulenger in his British Museum Catalogue of this order.

yet revealed to us. So strange, indeed, are they that some authorities have considered that the Ornithosaurs are entitled to rank as a distinct class; but they are essentially Reptiles, and agree in their intrinsic characters with the other two orders placed in the branch now under consideration. All their organisation is, however, modified for the purpose of flight through the air. Thus the body was supported during flight by a membranous expansion, or *patagium*, which was mainly borne by the greatly elongated phalangeals of the ulnar, or outermost digit of the manus (fig. 1095, marked iv); but which also extended along the sides of the body to embrace the hind limbs and tail (fig. 1098). The vertebræ are procœlous, and have their neuro-central suture obliterated; the precaudal series is not numerous; the cervicals are longer than the dorsals; and from three to six vertebræ are anchylosed together to form the sacrum. The cervical ribs in those cases where they have been observed are of the Crocodilian type. The skull (figs. 1096, 1097) is relatively large; and although more or less bird-like in general contour, yet maintains the reptilian type by the presence of the supratemporal fossæ, bounded by the junction of the postorbital with the squamosal bone. Bird-like resemblances are, however, shown by the circumstance that the bones of the skull anchylosed together at an early age; and that the two rami of the mandible were completely welded together at their symphysis. Moreover, as in Birds, the greater portion of the upper jaws is formed by the premaxillæ;

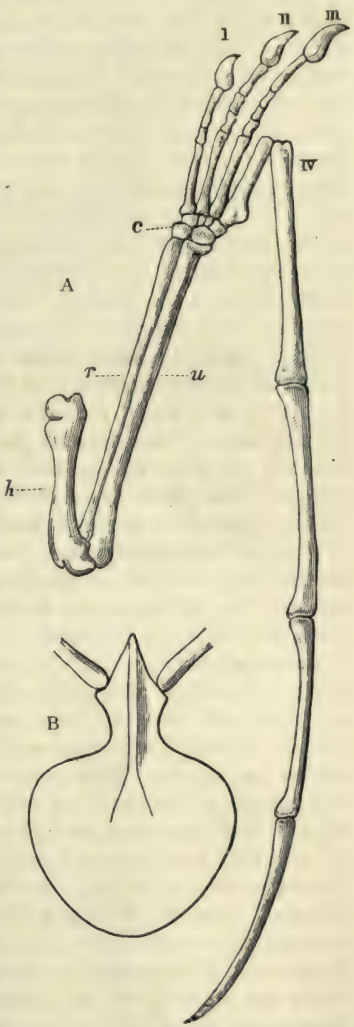

Fig. 1095. — A, Right pectoral limb of *Scaphognathus crassirostris*; B, Sternum and coracoids of *Pterodactylus*. *h*, Humerus; *r*, Radius; *u*, Ulna; *c*, Carpus; i–iv, Digits. These should have been numbered ii–v.

the nares are similarly approximated to the orbits, with the intervention of a preorbital vacuity, which (fig. 1096) may be very large; while the occipital condyle is situated on the base of the cranium; and the orbits are large, and there is generally an ossified ring in the sclerotic. The teeth are invariably simple and pointed; and are always implanted in separate sockets. In the pectoral girdle the scapula and coracoid are long and bird-like, and the latter has no fontanelle; there were no clavicles; but there was a broad heart-shaped sternum (fig. 1095, B), carrying a median keel superiorly. The angle of junction of the scapula and coracoid, as well as the keeled sternum, curiously resemble the corresponding parts in the skeleton of the Carinate Birds, and are consequently totally unlike those of the Ratitæ. The carpus consists of two main bones, one distal and the other proximal;[1] while on its radial side there is a small styliform ossification, regarded by Professors Owen and Marsh as the representative of the pollex—an identification which, if correct, will make the four remaining digits which are usually present the 2d, 3d, 4th, and 5th of the typical series, and not the 1st, 2d, 3d, and 4th as they are regarded by some writers (fig. 1095). The phalangeals of the ulnar digit, as already mentioned, are enormously elongated, and the terminal joint has no claw. The pelvis is relatively weak; and although the ilium is extended on both sides of the acetabulum, the structure of both this region and of the pelvic limbs is far removed from the avian type. Thus the pubis (or prepubis) is directed forwards, and the ischium is short and wide; while the pelvic limbs are relatively short. The fibula is, however, always fused with the tibia; and the astragalus may also unite with the latter bone; although the metatarsals always remain distinct both from one another, and also from the distal row of the tarsus. The greater number of the bones are hollow, and are frequently provided with pneumatic foramina, like those of Birds. The brain was bird-like, and the body was probably naked. In time this order ranges from the Lias to the Upper Chalk; and was especially abundant in the Upper Jurassic and Cretaceous strata of both the Old and New Worlds. Although the skeleton presents many remarkable resemblances to the Carinate Birds, yet these must be regarded as mainly due to adaptation for a similar mode of life; since it seems clear that the Pterodactyles are altogether off the direct line of the Avian pedigree.

Suborder 1. Pteranodontia. — In this suborder teeth are totally wanting, and the jaws were probably completely ensheathed in horn, like those of Birds. The skull (fig. 1096) has an enormous supraoccipital crest, projecting far behind the occiput; and the nares

[1] The carpus is erroneous in fig. 1095.

were completely confluent with the preorbital vacuities. According to Professor Marsh, these reptiles were mostly of gigantic size; some having a spread of wing of nearly or quite 25 feet. And in order to aid the powerful patagium in flight, the pectoral girdle was generally strengthened by the anchylosis of several vertebræ, and by the robust scapulæ articulating to the spines of these anchylosed

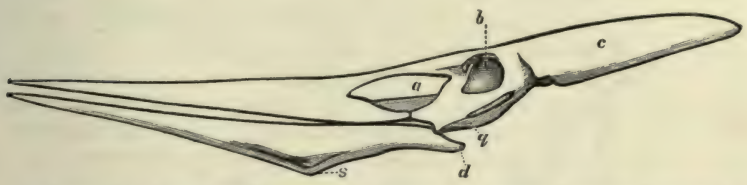

Fig. 1096.—Left lateral view of the skull of *Pteranodon longiceps;* from the Cretaceous of North America. One-twelfth natural size. *a*, Nares and preorbital vacuity; *b*, Orbit; *c*, Supraorbital crest; *d*, Angle of mandible; *q*, Quadrate; *s*, Symphysis (After Marsh.)

vertebræ; this peculiar feature being virtually a repetition of the pelvic girdle and sacrum on a much larger scale.

Family Pteranodontidæ.—The type genus *Pteranodon* (fig. 1096) occurs in the Cretaceous of North America; and although its members are generally of large size, it is also represented by one small species—*P. nanus*. The coracoid and scapula were united, but the oral aspects of the jaws have not the ridge and groove found in *Ornithochirus*. *Ornithostoma*, of the Cambridge Greensand, may have been an allied form. In *Nyctodactylus*, of the North American Cretaceous, Professor Marsh thinks that none of the dorsal vertebræ were anchylosed; and on this account the genus should perhaps form the type of a distinct family.

Suborder 2. Pterosauria.—In this, the typical, suborder teeth are present in both jaws; the cranium (fig. 1097) has no long supra-occipital crest directed backwards, and generally has the nares more or less completely separated from the preorbital vacuities. The scapula is (at least usually) not anchylosed to the neural spines of the dorsal vertebræ, which are distinct from one another. This suborder is mainly European.

Family Pterodactylidæ. — In the typical family the tail is short (fig. 1097); the jaws are toothed to their extremities; and the length of the metacarpus considerably exceeds half that of the ulna (fig. 1097). The skull, which is extremely bird-like, may be either long or short, and has the nares imperfectly separated from the preorbital vacuities; while in the pelvic limb the astragalus is always distinct from the tibia. In Europe this family is especially characteristic of the Upper Jurassic, and is abundantly represented in the Lower Kimeridgian lithographic limestones of Bavaria, which,

from their fine structure, have preserved not only the smallest bones, but not unfrequently also the impression of the membranous patagium. All the forms which can be certainly referred to this family are of small or moderate size. In *Ptenodraco*, of the lithographic limestones, we have a small Pterodactyle not larger than a sparrow, with a skull of very much the same contour as that of the latter, in

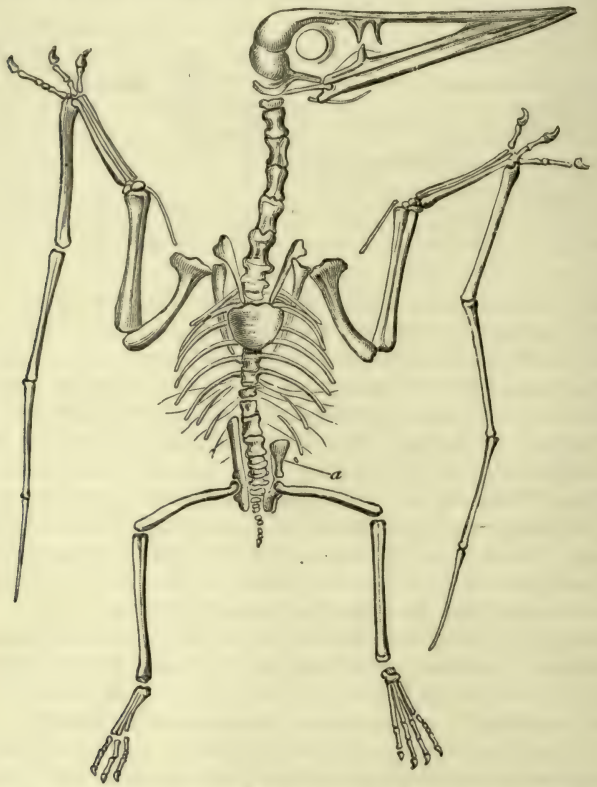

Fig. 1097.—Nearly entire skeleton of *Pterodactylus spectabilis*; from the Kimeridgian of Bavaria. The ventral aspect is shown; and on the right side the ilium, and on the left the pubis (*a*) is exposed.

which the teeth are confined to the extremities of the jaws, and the nares do not appear to be separated from the preorbital vacuities. *Pterodactylus* itself (of which *Ornithocephalus*[1] and *Diopecephalus*

[1] It has been proposed to take the name *Ornithocephalus* in place of *Ptenodraco*, a suggestion which is entirely opposed to all the rules of nomenclature. The first use of the former name in this sense was made by Fitzinger in 1826.

are synonyms), on the other hand, has the skull produced into a long beak or rostrum (fig. 1097), in which the teeth extend over a considerable space, and the large nares are slightly separated from the preorbital vacuities. The scapula is not anchylosed to the coracoid; and the pubes are short and rounded (fig. 1097). This genus appears to be confined to the lithographic limestones; the typical *P. antiquus* being about the dimensions of a woodcock.

Apparently allied to this genus is *Dermodactylus*, of the Jurassic of North America, in which the bones are said to have thicker walls. The type species is estimated to have had a spread of wing of from five to six feet. Finally, in *Cycnorhamphus*, of the Solenhofen limestones, we have a genus with a broad expanded beak, like that of a Swan, with the teeth confined to the anterior extremity. This genus is represented by a single species of comparatively large size, known as *C. suevicus*.

Here we may conveniently notice some gigantic Pterodactyles from the Cretaceous system of Europe, of which, owing to the exceedingly imperfect remains hitherto discovered, the family position must be left undetermined. Remains of some of those forms were originally regarded as belonging to Birds, and described under the names of *Palæornis* (Wealden) and *Cimoliornis* (Chalk). All these forms may be provisionally included under the generic name of *Ornithochirus*, although it is highly probable that some of them may really be distinct; and there does not at present appear any very good reasons for separating a Purbeck form for which the name *Doratorhynchus* has been proposed. Many of these Pterodactyles were of gigantic size; the spread of wing of some of the larger species being estimated at as much as 25 feet. Probably the tail was long; the jaws were toothed to their extremities, and frequently the upper anterior teeth curved forwards to project in advance of the muzzle. The oral surfaces of the upper and lower jaws were marked by a longitudinal ridge and groove; the skull was either short and stout, or much elongated; the scapula was often anchylosed to the coracoid; and in some instances the astragalus united with the tibia. It has also been suggested that *Ornithochirus* had but three digits in the manus, but this statement requires confirmation. The name *Cretornis* has been applied to the remains of *Ornithochirus* from the Chalk of Bohemia.

Family Rhamphorhynchidæ.—In this family the tail was at least usually long (as in fig. 1098); the extremities of the jaws were in many instances edentulous; and the length of the metacarpus was much less than half that of the ulna (fig. 1095). The skull (fig. 1099) was less bird-like than in the type family, with the nares separated by a distinct bar from the preorbital vacuity, and was

often comparatively short and stout; while in some instances the astragalus united with the tibia. This family certainly ranged from the Lias to the Upper Jurassic, but if *Ornithochirus* belong to it, its range must be extended to include the Cretaceous. In the genus *Scaphognathus* (fig. 1099) the teeth extend to the extremities of the jaws of the massive skull, in which the nares are separated by a broad bar from the larger preorbital vacuities. The tail of the type species is unknown, and in Goldfuss' restoration (fig. 1099) it was made like that of *Pterodactylus;* but Professor Zittel considers that it was elongated like that of *Rhamphorhynchus* and *Dimorphodon* (fig. 1101). The type species, which attains considerable dimensions, occurs in the Kimeridgian limestones of

Fig. 1098.—Restoration of *Dimorphodon macronyx*. Reduced. (After Owen.)

Bavaria, but the genus is also represented in the Upper Lias of Whitby. It is noteworthy that the peculiar form and relations of the jugal and quadratojugal found in the Dinosaurian genus *Diplodocus* (fig. 1076) also obtain in *Scaphognathus*. In *Rhamphorhynchus*, of the Kimeridgian of Bavaria, the extremities of the jaws are usually devoid of teeth; while in the hinder region the teeth incline forwards instead of having the nearly vertical direction of those of *Scaphognathus*. The scapula and coracoid were sometimes anchylosed; the astragalus was generally distinct from the tibia; the pes had either four or five digits; the pubes were slender, bent, and joined by a bony symphysis; while the long tail was strengthened by the ossification of its tendons. The membranous patagium developed a leaf-like expansion at the extremity of the tail,

as is beautifully shown in a specimen of the typical *R. Muensteri*, of which a restoration is shown in the accompanying woodcut.

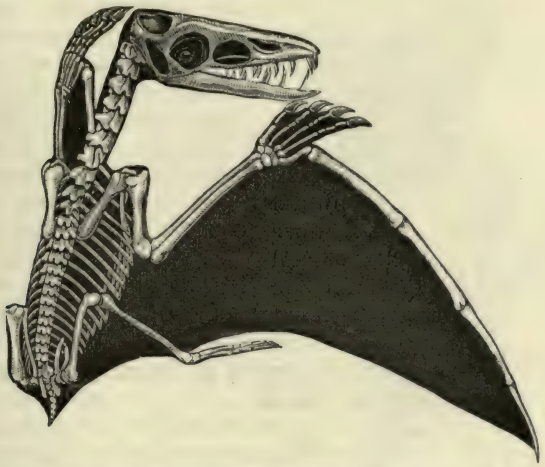

Fig. 1099.—The skeleton and patagium of *Scaphognathus crassirostris* according to the restoration of Goldfuss; from the Kimeridgian of Bavaria. Reduced. The presence of the first digit in the manus is incorrect; the tail should be long; while the patagium should have been more extended posteriorly, as in fig. 1098.

This species was of comparatively small size; but *R. grandis*, in which the astragalus united with the tibia, attained considerably larger dimensions. *Rhamphocephalus*, of the Lower Jurassic Stones-

Fig. 1100.—Restoration of *Rhamphorhynchus Muensteri* (*phyllurus*); from the Lower Kimeridgian of Bavaria. One-seventh natural size. (After Marsh.)

field slate, is distinguished from the preceding genus by the form of the teeth, and the great interorbital constriction of the cranium. *Dorygnathus*, from the Upper Lias of Germany, appears to

have been an allied genus. In the Lower Liassic genus *Dimorphodon* (fig. 1101) the jaws are toothed to their anterior extremities, and the hinder teeth of the mandible are much smaller than those in front. Both the nares and preorbital vacuities are of enormous size, and are separated by a narrow bar. The coracoid is anchylosed to the scapula; and the astragalus united to the tibia. *Dimorphodon* is thus the earliest known representative of the order; and the one species attained considerable dimensions. Its remains occur in the Liassic shales of Lyme Regis in Dorsetshire, and were first brought to notice in 1822 by the indefatigable Dean Buckland.

Fig. 1101. — Restored skeleton of *Dimorphodon macronyx*; from the Lower Lias. Reduced. *f*, Ulnar digit; *m*, Other digits; *p*, Metatarsus. (After Owen.)

Ordinal Position Uncertain.— Here may be noticed a genus of which the serial position must for the present remain undecided. It is known as *Ornithodesmus*, and was founded upon an imperfect sacrum from the English Wealden, which has been regarded as Avian, although its right to distinction from the Ornithosauria appears by no means certain. It may be observed that the so-called *Ornithopterus*, of the Upper Jurassic limestones of Bavaria, said to be characterised by the presence of only two digits in the ulnar digit of the manus, and which has been regarded as Avian, appears to have been founded upon an imperfect specimen of *Rhamphorhynchus*; and it may also be mentioned that the name *Ornithopterus* is preoccupied by the Lepidopterous genus *Ornithoptera*. Finally, it has been suggested that a tooth from the Trias of Italy described under the name of *Tribelesodon* may indicate an Ornithosaurian at that early period, but the evidence in support of that view is at present wholly insufficient.

LITERATURE OF REPTILIA.

1. BAUR (G.)—"On the Phylogenetic Arrangement of the Sauropsida." 'Journal of Morphology,' vol. i. (1887).
2. BOULENGER (G. A.)—"Catalogue of Chelonians, &c., in the British Museum" (1889).
3. BUCKLAND (W.)—"Geology and Mineralogy" (1837).
4. COPE (E. D.)—"Extinct Batrachia, Reptilia, and Aves of North America." 'Trans. Amer. Phil. Soc.,' vol. xiv. p. 100 (1871).
5. —— "Homologies of the Cranial Bones of the Reptilia, and the Systematic Arrangement of the Class." 'Proc. Amer. Assoc.' for 1870.
6. —— "The Relations between the Theromorphous Reptiles and the Monotreme Mammalia." 'Proc. Amer. Assoc.' for 1884.
7. —— "The Vertebrata of the Cretaceous Formations of the West." 'Rep. U.S. Geol. Surv. Terrs.,' vol. ii. (1875).
   See also numerous memoirs in various American serials.
8. CREDNER (H.)—"Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen'schen Grundes bei Dresden." 'Zeitschr. deutsch. geol. Gesellschaft.' 1881-88.
9. DESLONGCHAMPS (E.)—"Notes Paléontologiques" (1863-69).
10. DOLLO (L.)—"Note sur les Dinosauriens de Bernissart," 5 parts. 'Bull. Mus. R. d'Hist. Nat. Belg.' 1882-84.
    —— "Note sur l'Osteologie des Mosasauridæ." *Ibid.* 1882.
    See also other memoirs in same and other serials.
11. GÜNTHER (A.) and MIVART (ST G.)—"Reptilia." 'Encyclopædia Britannica,' 9th ed.
12. HULKE (J. W.)—"Presidential Addresses to the Geological Society." 1883-84.
13. —— "Supplemental Note on *Polacanthus Foxii*." 'Phil. Trans.' 1887, pp. 167-172, pl. viii.
14. —— "Contributions to the Skeletal Anatomy of the Mesosuchia, based on fossil remains from the clays near Peterborough, in the collection of A. N. Leeds, Esq." 'Proc. Zool. Soc.' 1888.
    See also other memoirs in 'Phil. Trans.' and 'Quart. Journ. Geol. Soc.'
15. HUXLEY (T. H.)—"A Manual of the Anatomy of Vertebrated Animals," 2d ed. London. 1871.
16. —— "On the Affinities between Dinosaurian Reptiles and Birds." 'Quart. Journ. Geol. Soc.,' vol. xxvi. (1870).
17. —— "On the Classification of the Dinosauria," *tom. cit.*
18. —— "On *Stagonolepis* and the Evolution of the Crocodilia," *ibid.*, vol. xxxi. (1875).
19. —— "On *Hyperodapedon*." *Ibid.*, vol. xliii. (1887).
    See also numerous memoirs in the same and other serials.
20. KIPRIJANOFF (W.)—"Studien über die Fossilen Reptilien Russlands." 'Mém. Ac. Imp. St Pétersburg,' vols. xxviii.-xxxi. (1881-83).
21. KOKEN (E.)—"Die Dinosaurier, Crocodiliden, und Sauropterygier des Norddeutschen Wealden." 'Pal. Abhandl.,' vol. iii., pt. 5 (1887).
22. LEIDY (J.)—"Cretaceous Reptiles of the United States." 'Smiths. Contrib. Knowl.,' vol. xiv. (1864).

23. LEIDY (J.)—"Contributions to the Extinct Vertebrate Fauna of the Western Territories." 'Rep. U.S. Geol. Surv. Terrs.,' vol. i. (1873).
24. LYDEKKER (R.)—"Catalogue of Fossil Reptilia and Amphibia in the British Museum." Parts i., ii., iii. (1888-89).
25. —— "Indian Pretertiary Vertebrata." 'Palæontologia Indica,' ser. 4, vol. i., pts. 3-5 (1879-85).
26. —— "Indian Tertiary and Post-Tertiary Vertebrata." *Ibid.*, ser. 10, vol. iii., pts. 6, 7 (1885-86).
27. —— "On Eocene and Mesozoic Chelonia and a tooth of (?) *Ornithopsis*." 'Quart. Journ. Geol. Soc.,' vol. xlv. (1889).
28. MARSH (O. C.)—"Classification of the Dinosauria." 'American Journal of Science,' ser. 3, vol. xxiii. (1882), and 'Rep. Brit. Assoc.' for 1884.
29. —— "Principal Characters of American Jurassic Dinosaurs." 8 parts. *Ibid.*, vols. xvi.-xxvii. (1878-84).
30. —— "Principal Characters of American Cretaceous Pterodactyles." *Ibid.*, vol. xxvii. (1884).
31. —— "Structure of the Skull and Limbs in Mosasauroid Reptiles." *Ibid.*, vol. iii. (1872).
32. MEYER (H. VON).—"Saurier des Muschelkalkes." (1847-55.)
33. —— "Saurier aus dem Kupfer-Schiefer der Zechstein-formation." (1856.)
34. OWEN (R.)—"Descriptive Catalogue of the Fossil Reptilia and Fishes in the Museum of the Royal College of Surgeons of England." (1854.)
35. —— "Catalogue of the Fossil Reptiles of South Africa in the Collection of the British Museum." (1876.)
36. —— "Monograph on the Fossil Reptilia of the London Clay." Part i., Chelonia (Owen and Bell). 'Palæontographical Society.' (1849.) Part ii., Crocodilia and Ophidia. *Ibid.* (1850.)
37. —— "Monograph on the Fossil Reptilia of the Wealden and Purbeck Formations." *Ibid.* (1853-59, and Supplements extending to 1876.)
38. —— "Monograph on the British Fossil Reptilia of the Oolitic Formations." *Ibid.* (1861.)
39. —— "Monograph on the Fossil Reptiles of the Cretaceous Formation." *Ibid.* (1851-64.)
40. —— "Monograph of the Fossil Reptilia of the Liassic Formations." *Ibid.* (1865 and 1870.)
41. —— "Monograph of the British Fossil Reptilia of the Kimmeridge Clay." *Ibid.* (1869.)
42. —— "Monograph of the British Mesozoic Reptilia." *Ibid.* (1873, 1875, and 1877.)
43. —— "Odontography." (1840-45.)
44. —— "Report on Fossil Reptiles." 'Rep. Brit. Assoc.' for 1839 and 1841.
45. —— "On Dicynodon." 'Trans. Geol. Soc.,' ser. 2, vol. vii. (1845).
46. —— "History of British Fossil Reptiles." (1849-84.)
47. —— "On Parts of the Skeleton of *Meiolania platyceps*." 'Phil. Trans.' 1888.
48. PHILLIPS (J.)—"Geology of Oxford and the Valley of the Thames." *Oxford.* 1871.
49. RILEY (H.) and STUTCHBURY (S.)—"Description of Remains of Saurian Animals from the Magnesian Conglomerate of Bristol." 'Trans. Geol. Soc.,' ser. 2, vol. v. (1840).

50. SEELEY (H. G.)—"On the Dinosauria of the Cambridge Greensand." 'Quart. Journ. Geol. Soc.,' vol. xxxv. (1879).
51. —— "On the Reptile Fauna of the Gosau Formation." *Ibid.*, vol. xxxvii. (1881).
52. —— "On the Dinosaurs of the Maastricht Beds." *Ibid.*, vol. xxxix. (1883).
53. —— "On the Mode of Reproduction of certain species of *Ichthyosaurus*." 'Rep. Brit. Assoc.' for 1880.
54. —— "Researches on the Structure, Organisation, and Classification of the Fossil Reptilia." Part i., *Protorosaurus Speneri;* part ii., *Pareiasaurus bombidens*. 'Phil. Trans.' 1887-88.
55. —— "Index to the Fossil Remains of Aves, Ornithosauria, and Reptilia in the Woodwardian Museum." *Cambridge*. 1869.
56. —— "The Ornithosauria." *Cambridge*. 1870.
See also numerous other memoirs in the above and other serials.
57. SOLLAS (W. J.)—"On a new Species of *Plesiosaurus*, accompanied by a Supplement on the Distribution of the Genus." 'Quart. Journ. Geol. Soc.,' vol. xxxvii. (1881).
58. WOODWARD (A. S.)—"The History of Fossil Crocodiles." 'Proc. Geol. Assoc.,' vol. ix. (1886.)

CHAPTER LVI.

CLASS AVES.

General Structure.

The fifth class of the Vertebrata is that of Aves, or Birds, which, as we have already mentioned under the description of the class Reptilia, presents a number of characters in common with the latter. Birds, indeed, as Professor Huxley remarks, are animals so similar to Reptiles in all the most essential features of their organisation, that they may be said to be merely an extremely modified and aberrant Reptilian type. Their differentiation is, however, so great as to indicate without doubt their right to form a distinct class. It will be unnecessary to recapitulate the characters common to Birds and Reptiles—together constituting the province Sauropsida—and we may accordingly proceed to note the distinctive features of the former class. It may be well, however, to observe before proceeding further that, according to the arrangement proposed by Professor A. Newton, Birds are divided into three primary divisions or orders, respectively known as Saururæ, Ratitæ, and Carinatæ; the fossil representatives of which will be noticed in the next chapter.

In the first place, all Birds, so far as can be ascertained, were provided with the peculiar epidermal covering known as feathers, which are totally unknown among the Reptiles; while ossifications in the dermis are extremely rare, and never take the form of bony scutes. No Bird, again, has procœlous vertebræ; while in all existing forms the centra of the cervicals have cylindroidal, saddle-shaped, articular surfaces, although these are amphicœlous in certain Mesozoic forms. In no cases are there sacral ribs for attachment of the ilia in the proper sacral vertebræ. The sternum has no backwardly-produced median processes for the ribs; all of which are attached superiorly to its lateral borders. If an interclavicle ever exists, it is fused with the clavicles into a compound bone

termed the furcula (fig. 1106). No Bird has more than three digits in the manus; all of which may be furnished with claws. The three elements of the pelvis are nearly always anchylosed together in the adult (fig. 1102); the ilium being produced in advance of the acetabulum (of which the inner wall is unossified), and the ischium and pubis directed backwards, in a more or less parallel direction, and only very rarely meeting in a ventral symphysis. The proximal row of the tarsus is always united with the tibia to form a tibio-tarsus; while the distal row coalesces with the

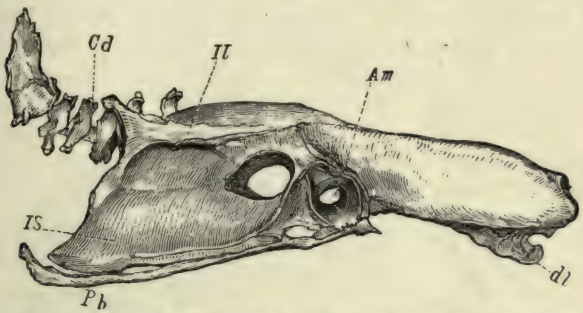

Fig. 1102.—Right lateral view of the pelvis and caudal vertebræ of a Fowl (*Gallus*). *Il*, Ilium; *Is*, Ischium; *Pb*, Pubis; *Am*, Acetabulum; *dl*, Dorso-lumbar vertebræ; *Cd*, Caudal do.

three median metatarsals to constitute a tarso-metatarsus. In all recent Birds only the right aortic arch is present; the arterial and venous circulations meeting only in the capillaries; and the blood is hot.

Some of the above characters are common to certain Reptiles; and it is only the whole of them collectively which can be regarded as characteristic of Birds as a class.

Noticing in rather more detail certain features of the osteology, it may be observed that the skeleton is usually remarkable for its combination of compactness and lightness, and also by the permeation of the greater number of the bones by air-cavities. The skull (fig. 1103) is formed on the general reptilian type, but is remarkable for the greater relative development of the brain-case, although this feature is nearly paralleled in the Ornithosauria. The component bones have a great tendency to unite in the adult by the obliteration of their sutures, and their texture is delicate and spongy, and totally unlike the ivory-like structure so generally observable among Reptiles. The single occipital condyle, which is mainly formed by the basioccipital, is not placed at the hinder extremity of the cranium, but becomes shifted forwards and downwards, so that the basal axis of the latter forms an angle with the axis of the

vertebral column. In Reptiles a similar feature occurs in the Ornithosauria. The inferior temporal arcade, formed by the jugal and quadratojugal (fig. 1103), and connecting the maxilla with the quadrate, is invariably present, but the superior temporal arcade is always wanting; and there are never distinct postorbitals or postfrontals. The complete inclusion of the parietals in the roof of the brain-case prevents the formation of the posttemporal fossæ, which constitute such a characteristic feature in the skulls of the majority of Reptiles; and no Bird has a parietal foramen. The base of the cranium is formed by the basioccipital and basisphenoid, from the latter of which proceeds the rod-like sphenoidal rostrum, representing the anterior part of the parasphenoid; while the posterior portion

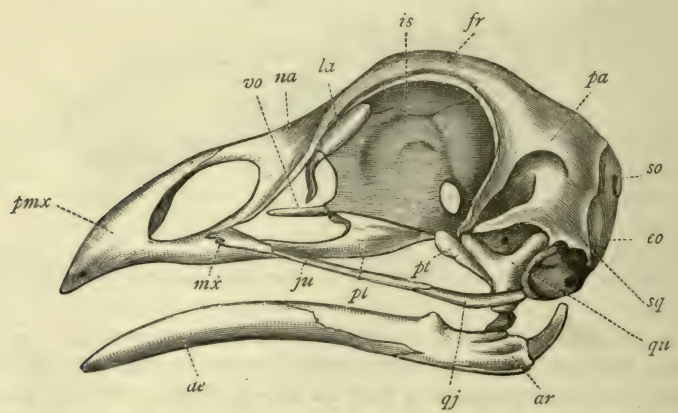

Fig. 1103.—Left lateral view of the skull of the Fowl. *de*, Dentary portion of the mandible; *ar*, Articular portion of do.; *qu*, Quadrate; *sq*, Squamosal; *eo*, Exoccipital; *so*, Supraoccipital; *pa*, Parietal; *fr*, Frontal; *la*, Lachrymal; *na*, Nasal; *vo*, Vomer; *pmx*, Premaxilla; *mx*, Maxilla; *ju*, Jugal; *qj*, Quadratojugal; *pt*, Pterygoid; *pl*, Palatine; *is*, Interorbital septum.

of the latter persists in the basitemporal plate underlying the basioccipital and basisphenoid. There is always a preorbital (lachrymonasal) vacuity between the nasal, lachrymal, and maxilla (the triangular space immediately behind the nasals in fig. 1103), as in many extinct Reptiles; and the interorbital septum is always more or less ossified. The narial aperture (fig. 1103) is lateral, and nearly always placed a short distance in advance of the orbit near the root of the beak. The greater portion of the latter is formed, as in the Ornithosauria, by the premaxillæ, which coalesce at a very early period in the middle line, and thus form a triradiate bone, giving off a median nasal and a pair of lateral maxillary processes. The pterygoids (fig. 1103) never unite together in the middle line to form a completely closed palate; and neither those bones nor the palatines ever develop inferior palatal plates to separate the narial

passage from the mouth. In this respect, therefore, the development of the Bird's skull does not attain such a specialisation as that of the existing Crocodiles. The quadrate is usually movably attached to the squamosal; and the articulation of the palatopterygoid bar to the basipterygoid processes of the sphenoidal rostrum is also a movable one, by which means the premaxillary beak can be moved to a certain extent upon the rest of the skull. The vomers are subject to great variation. They underlie the ethmosphenoidal region, and when present are connected posteriorly with the palatines, except in the Ostrich. The relations of these and the other bones of the palate form important features in Professor Huxley's classification of Birds; but since this is a subject to which the attention of the Palæontologist is but seldom directed, the reader desirous of further information must refer to other works. The jugal and the quadratojugal are slender, rod-like bones, of which the former articulates with the equally slender maxilla, and the latter by a hollow surface with the quadrate. In all existing Birds the dentary elements of the two rami of the mandible are always found welded at the symphysis into a single bone; but in the Cretaceous *Ichthyornis*, and perhaps in other Mesozoic forms, this union is imperfect. There is frequently a lateral vacuity between the dentary and splenial, like that of the Crocodilia. The angle of the mandible may be either truncated, or produced into a long recurved process, as in the Fowls (fig. 1103), Ducks, and Geese. In existing and Tertiary Birds the beak is ensheathed in horn, and is totally devoid of teeth; but rudiments of teeth have been found in some Parrots. And in certain Mesozoic forms the premaxilla, maxilla, and dentary bones were furnished with a complete series of sharp teeth. A ring of bones is always developed in the sclerotic of the eye.

In some Mesozoic Birds the vertebral centra were amphicœlous, but in all others the vertebræ exhibit certain well-marked peculiarities. Thus the neural articulations are always well developed, and the arch is invariably articulated to the centrum. The neck is usually very long; the number of its vertebræ ranging from eight to twenty-three. The atlas vertebra forms a thin ring, in which the transverse ligament may be ossified; and the axis always has the odontoid process anchylosed to it. The succeeding cervicals have either short neural spines, or no spines at all; the anterior surfaces of their centra are cylindroidal and convex from above downwards, and concave from side to side, the reverse condition obtaining posteriorly (fig. 1104). These surfaces are usually described as saddle-shaped;[1] and there may be a hæmal spine inferiorly. In the imma-

[1] The term *heterocœlous* has been proposed for this type of vertebral structure.

ture Ratitæ the cervicals have ribs articulating with an upper and a lower process, as in the Crocodilia; and in the adult (fig. 1104) these ribs anchylose to the vertebræ, and thus resemble perforated transverse processes, in which the canal (*f*) serves for the protection of the vertebral artery.[1] In adult Carinatæ these lateral arches, as they may be termed, become further modified, and develop prolongations for the protection of other parts of the vasculo-neural system. The dorsal vertebræ are liable to variation in number; their centra usually resemble those of the cervical region, but in the Penguins the articular surfaces of some may be spheroidal an-

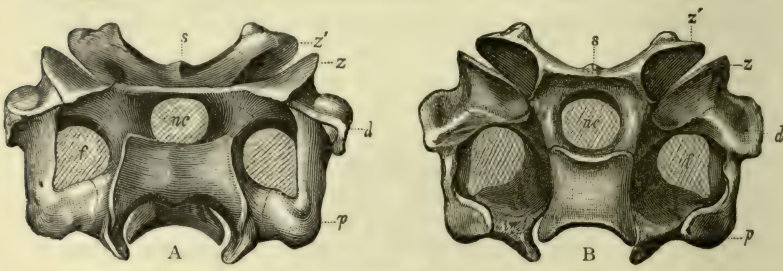

Fig. 1104.—(A) Anterior and (B) posterior views of a cervical vertebra of *Hesperornis regalis*; from the Cretaceous of North America. *s*, Neural spine; *z*, Prezygapophysis; *z'*, Postzygapophysis; *d*, Transverse process, or diapophysis; *p*, Rib-facet, or parapophysis; *nc*, Neural canal; *f*, Costal canal. (After Marsh.)

teriorly.[2] They usually have well-marked neural, and may or may not have inferior median spines; and they are in some instances anchylosed together, but in others are susceptible of a limited amount of motion. Throughout the whole dorsal series there is a well-developed transverse process from the arch for the tuberculum of the rib; while the centrum has a lateral facet for the capitulum. The method of costal articulation resembles, therefore, that obtaining in the first two dorsal vertebræ of the Crocodilia. These features are characteristic of all Birds. The dorsal vertebræ are succeeded posteriorly by a number of anchylosed vertebræ forming the sacrum. According, however, to the researches of Dr Gadow, only two or three of these vertebræ are truly sacral; those in front belonging to the lumbar, and those behind to the caudal region. Of the proper sacrals the two hindmost correspond to those of the Crocodilia, and the second of these to the single sacral of the Amphibia. The vertebræ articulating with the ilia do not develop ribs, but articulate

[1] This arrangement of the ribs is precisely similar to that occurring in certain Dinosaurs, as is shown in fig. 1071 (p. 1170).

[2] Certain Water and Wading Birds as well as Parrots, and the remarkable *Steatornis* have opisthocœlous dorsal vertebræ. The Parrots also have epiphyses to these vertebræ.

by transverse processes placed on the arch. The anchylosed series of caudals, which are sometimes termed *uro-sacral*, are in some instances, as in *Archæopteryx* and *Rhea*, followed by a considerable number of free vertebræ, but more usually by only a few, succeeded by a triangular terminal bone, known as the *pygostyle* (fig. 1106), which carries the tail feathers and glands, and represents several coalesced vertebræ. In no known Birds are ossified intercentral elements developed, with the exception of the inferior bar of the atlas vertebra. Nearly all the dorsal ribs develop tubercular and capitular processes, and some have also uncinate processes (fig. 1106, *up*). The sternum has a pair of grooves superiorly for the reception of the coracoids; and in the Ratitæ (fig. 1105) it is rhomboidal and convex, without trace of a median keel, its development taking place from two lateral centres. In the majority of Carinatæ the sternum (fig. 1106, *st*) is, however, elongated, and has a strong median keel for the attachment of the pectoral muscles. In this type two membranous vacuities frequently exist in the posterior portion, which in the dry skeleton form holes or notches, separated by bony processes, which represent divisions of the Mammalian xiphisternum. In many Carinatæ, and especially the Passerines, there are also developed a median manubrium sterni, and lateral costal processes for the attachment of the ribs. The coracoid (fig. 1106, *c*) in the Carinatæ is an elongated bone more like that of Crocodiles than that of Dinosaurs; it has no fontanelle, and articulates at an acute angle with the scapula, from which it usually remains distinct. It takes an equal share with the latter in the formation of the glenoid cavity for the head of the humerus, and at its distal end may overlap its fellow. In the Ratitæ the coracoid (fig. 1111) is, however, generally shorter and more Dinosaurian-like, and may have a fontanelle, while its long axis is either coincident or parallel with that of the adjacent portion of the scapula, with which it is invariably anchylosed in the adult. The scapula in Carinate Birds (fig. 1106, *s*) consists of a thin and narrow plate of bone, often extending backwards to a considerable length, and without any suprascapula. Occasionally an additional bony rod is developed on the outer side of the scapula. The glenoidal ends of both the scapula and coracoid are divided into a glenoidal and a clavicular process in this order. In the same order the clavicle is nearly always well developed, and fuses with its fellow to form the U-shaped furcula (fig. 1106, *fu*); but in the Ratitæ

Fig. 1105.—Sternal region of the Ostrich (*Struthio*). Reduced. *s*, Scapula; *c*, Coracoid.

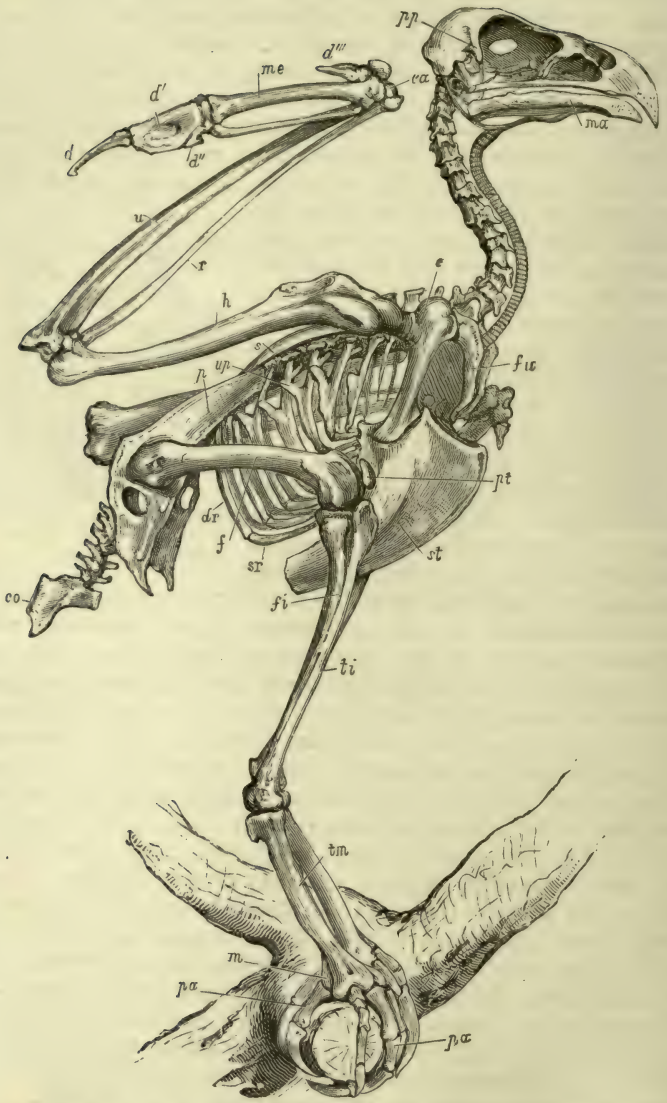

Fig. 1106.—Skeleton of Eagle (*Aquila*). Reduced. *pp*, Postorbital process; *ma*, Mandible; *st*, Sternum; *dr*, Rib; *sr*, Sternal do.; *up*, Uncinate process; *co*, Pygostyle; *fu*, Furcula; *c*, Coracoid; *s*, Scapula; *h*, Humerus; *r*, Radius; *u*, Ulna; *ca*, Carpus; *mc*, Metacarpus; *d'''*, Pollex; *d*, *d'*, Phalangeals of first digit; *d''*, Do. of second do.; *p*, Ilium; *f*, Femur; *pt*, Patella; *ti*, Tibia; *fi*, Fibula; *tm*, Tarsometatarsus; *m*, First metatarsal; *pa*, Phalangeals. (After Milne-Edwards.)

the clavicles are rudimentary or wanting, and never unite to form a furcula. No Bird preserves a distinct interclavicle, although it has been thought that the median portion of the furcula represents this element—a view which, from developmental considerations, is now regarded as improbable. The furcula itself may anchylose with either the manubrium of the sternum, or with the coracoids; and very rarely both these unions occur together.

In the pectoral limb the component bones, when at rest, have been greatly altered from their original primitive position; the change being somewhat greater than that occurring in the majority of Mammals. The humerus of Carinates (fig. 1106, *h*) is expanded at both ends; the proximal extremity having a strong preaxial delto-pectoral ridge for the pectoral muscle. The pneumatic foramen occurs on the proper dorsal aspect; and at the distal extremity the prominent oblique condyle, on the outer side of the palmar aspect for the articulation of the radius, forms a very characteristic feature. In the Ratitæ this bone has less distinctive characters, and may be very small, or even absent. There is no foramen for vessels at the distal extremity of the humerus in any member of the class. The radius and ulna (fig. 1106, *u*, *r*) are always separate; the former, which is usually the larger of the two, being frequently marked with a line of tubercles for the attachment of the secondary wing-feathers. In the adult of recent Birds the free bones of the carpus are reduced to two—a radiale and ulnare; but in the Jurassic *Archæopteryx* only the radiale remains. In the latter genus the manus comprises three free metacarpals and digits; of which the first carried two, the second three, and the third four phalangeals; the terminal bone in each digit being furnished with a claw. In existing Carinate Birds the three metacarpals (fig. 1106) are more or less completely fused together; and, according to Professor Weinsheimer, ten families possess the same number (two) of phalangeals in the first digit as in *Archæopteryx*, the distal one bearing a claw; while four families also possess three phalangeals in the second digit, like *Archæopteryx*, but in only two of these families is the terminal phalangeal provided with a claw. In all existing Carinates the third digit has only a single phalangeal, without a claw. Among the Ratitæ there are three digits in *Struthio* and *Rhea*; but *Apteryx* and *Casuarius* have but a single digit, which is clawed. There is usually an interspace between the curved second and third metacarpals which may be filled up by a thin plate of bone.

The characters of the pelvis have been already briefly alluded to. The ilium (fig. 1107) is always produced considerably on both sides of the acetabulum, and in some cases, as in the Apteryx, the anterior production is very great; it articulates with the long sacrum, of which the homology has been already noticed. The ilium arches

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over the greater part of the acetabulum, of which, as already mentioned, the centre is unossified, and has an external articular surface for the great trochanter of the femur termed the *antitrochanter*. The ischium forms the hinder half of the inferior part of the acetabulum, and is a moderately broad bar of bone directed downwards and backwards, or occasionally backwards (fig. 1112). In the Carinatæ (fig. 1102) it generally unites inferiorly with the ilium, by which means the upper part of the ilio-ischiatic notch is converted into a foramen; but in the Ratitæ (figs. 1107, 1112) there is no such union. In *Rhea* alone, among existing Birds, the ischia unite in a ventral symphysis. The pubis is generally a long and slender

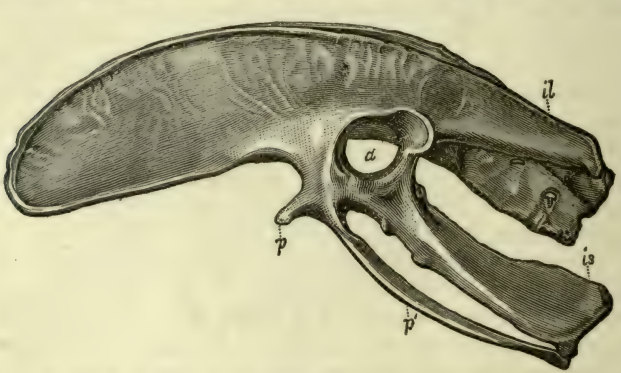


Fig. 1107.—Left side of the pelvis of the Emeu (*Dromæus*). Reduced. *il*, Ilium; *is*, Ischium; *p'*, Pubis; *p*, Pectineal process of do.; *a*, Acetabulum. (After Marsh.)

bone running parallel to the ischium, and entering into the anterior part of the lower border of the acetabulum; it frequently gives off a pectineal process (fig. 1107), which is apparently homologous with the preacetabular process of the pubis of the Ornithopodous Dinosauria. The Ostrich (*Struthio*) is peculiar among living Birds in having a symphysis pubis; while in *Archæopteryx* alone are the three pelvic bones separate. The femur is a short thick bone, with its head placed at right angles to the shaft, as in certain Dinosauria. Its condyles are large, and antero-posteriorly elongated. A patella is frequently present, and may be double. The fibula is always imperfect distally, and may be completely anchylosed to the tibia. The latter, or tibio-tarsus as it should be correctly termed, is a very characteristic bone; and is always longer than the femur. Proximally this bone is expanded and produced into an anterior cnemial process, like that of the Dinosauria, which may extend above the knee-joint; and the distal extremity (fig. 1108, A) has a trochlea-like surface, and consists of the astragalus of the tarsus, which has been completely fused with the tibia. On the anterior surface of

this bone, above the astragalus, there is frequently (as in fig. 1108, A) a bony bridge over the channel for the extensor tendons of the foot. The tarso-metatarsus (fig. 1106, *tm*) immediately succeeds the tibia; and consists proximally of the distal portion of the tarsus, with which the three middle metatarsals of the typical foot are usually completely welded to form a rod-like bone, generally terminating in three distal pulley-like surfaces for the articulation of the phalangeals. In the Penguins, however, intervals exist between the three component bones of the shaft; and in the Ostrich only two metatarsals enter into the compound element. Generally the median metatarsal at its distal end is thrust somewhat in advance of the other two (fig. 1108, B). The form of the distal condyles of this bone is very characteristic of different groups of Birds. In cases where the hallux, or first digit, is developed it is only the distal portion of its metatarsus which is attached to the posterior aspect of the tarso-metatarsus. No adult Bird has any trace of a fifth digit, and the number of digits may vary from two (Ostrich) to four (Parrots). In four-toed Birds the phalangeals generally number 2, 3, 4, 5, reckoning from the first (hallux) to the fourth digit.

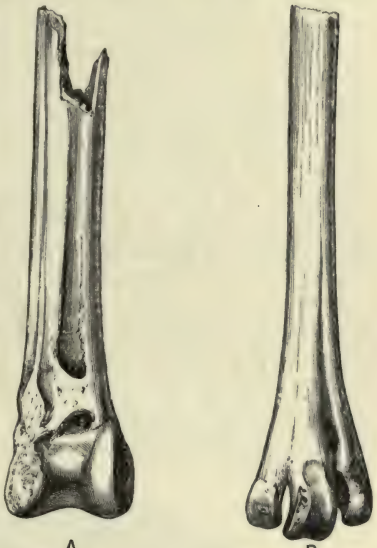


Fig. 1108.—*Ibis melanocephala*. The distal portion of the right tibio-tarsus (A) and left tarso-metatarsus (B).

This increase in an arithmetical ratio of the phalangeals of the toes, in proceeding from the inner to the outer side of the foot, obtains in almost all Birds, and enables us readily to detect which digit is suppressed, when the normal four are not all present. Variations of different kinds exist, however, in the number and disposition of the toes. In many Birds—such as the Parrots—the outermost toe is turned backwards, so that there are two toes in front and two behind; whilst in the Trogons the inner toe is turned back with the hallux, and the outermost one is turned forwards. In others, again, the outer toe is normally directed forwards, but can be turned backwards at the will of the animal. In the Swifts, on the other hand, all four toes are present, but they are all turned forwards. In many cases—especially amongst the Anserine birds—the hallux is wholly wanting, or rudimentary. In the Emeu, Cassowary, Bustards, and other genera, the hallux is invariably absent, and the foot is three-toed. In the

Ostrich both the hallux and the second toe are wanting, and the foot consists simply of the third and fourth digits.

In regard to their geological distribution it should be observed that the remains of Birds are generally by no means so common in ossiferous deposits as those of Mammals. This scarcity is probably in part due to the comparatively small size and fragile nature of the bones of a large number of members of the class; and also, as Sir C. Lyell has observed, to the circumstance that "the powers of flight possessed by most birds would ensure them against perishing by numerous casualties to which quadrupeds are exposed during floods;" so that, "if they chance to be drowned, or to die when swimming on water, it will scarcely ever happen that they will be submerged so as to become preserved in sedimentary deposits, since, from the lightness of the bones, the carcass would remain long afloat, and would be liable to be devoured by predaceous animals." To these considerations must be added the absence of teeth in the great majority of Birds, whereby we are deprived of evidence which in the case of Mammals has thrown most important light upon the nature and affinity of fossil forms.

The earliest suggestion of the occurrence of Birds is afforded by impressions of huge Sauropsidan feet (fig. 1109) found in the

Fig. 1109.—Sauropsidan footprint, and impressions of rain-drops; from the Trias of the Connecticut Valley. Reduced.

reputed Triassic sandstone of the Connecticut Valley in the United States. These impressions were evidently made either by Ornithopodous Dinosaurs, or by Ratite Birds; and the occurrence of certain reptilian bones in the same deposits indicates that at least some of them are probably of Dinosaurian origin. The absence of the

impression of a tail among some of these tracks renders it, however, not altogether improbable that a few of them may be due to Birds.

Apart from the foregoing extremely doubtful evidence, the earliest undoubted occurrence of Birds is in the Upper Jurassic, where we find *Archæopteryx* in the Kimeridgian of Bavaria. *Laopteryx*, from the Jurassic of North America, which was described as a Bird, is more probably a Reptile. Of the extremely generalised nature of the former mention is made in the next chapter. In the Cretaceous system of North America we find not only the remarkable toothed Birds, which were already differentiated into the Ratite and Carinate modifications; but there were apparently others more nearly allied to existing types. Bird-remains also occur rarely, and in a very fragmentary state, in the Upper Cretaceous of Europe. With the Eocene we enter upon an Avian fauna of a decidedly modern type; and at the period of the Lower Miocene the greater number of existing suborders were well represented.

We are at present to a great extent in the dark as to the manner in which Birds branched off from the primitive Sauropsidan stock; but it is pretty evident that the Dinosauria are those Reptiles most nearly related to Birds, and that the Ornithosauria are totally out of the direct ancestral line,—the curious resemblance which they present to Carinate Birds being apparently solely due to their somewhat similar mode of life.

In respect to the mode of origin of the Ratite and Carinate modifications of Bird-structure, we may quote from an admirable article by Professor A. Newton, who observes that—"First of all we find that while Birds still possessed the teeth they had inherited from their Reptilian ancestors, two remarkable and very distinct types of the class had already made their appearance, and we must note that these two types are those which persist at the present day, and even now divide the class into the Ratitæ and Carinatæ. Furthermore, while the Ratite type (*Hesperornis*) presents the kind of teeth, arrayed in grooves, which indicate (in Reptiles at least) a low morphological rank, the Carinate type (*Ichthyornis*) is furnished with teeth set in sockets and showing a higher development. On the other hand, this early Carinate type has vertebræ, whose comparatively simple biconcave form is equally evidence of a rank unquestionably low; but the saddle-shaped vertebræ of the contemporary Ratite type as surely testify to a more exalted position. Reference has been already made to this complicated if not contradictory state of things; the true explanation of which seems to be out of reach at present. It has been for some time a question whether the Ratite is a degraded type descended from the Carinate, or the Carinate a superior development of the Ratite type." The Professor, after noticing that many Zoologists have adopted the former view, proceeds to observe that, before the question can be answered, a reply must be given to the following question—"Was the first animal which any one could properly call a 'Bird,' as distinguished from a 'Reptile,' possessed of a keeled sternum or not? Now Birds would seem to have been differentiated from Reptiles while the latter had biconcave vertebræ, and teeth whose mode of attachment to

the jaw was still variable. There is no reason to think that at that period any Reptile (with the exception of Pterodactyles, which, as has already been said, are certainly not in the line of Birds' ancestors) had a keeled sternum. Hence it seems almost impossible that the first Bird should have had one; that is to say, it must have been practically of the Ratite type. Professor Marsh has shown that there is good reason for believing that the power of flight was gradually acquired by Birds, and with that power would be associated the development of a keel to the sternum, on which the volant faculty so much depends. . . . Thus the Carinate type would, from all we can see at present, appear to have been evolved from the Ratite." After observing that embryological and distributional facts afford support to this view, Professor Newton continues as follows: "No doubt the difficulty presented by the biconcave vertebræ of the earliest known representative of the Carinate type is a considerable obstacle to the view just taken. But Professor Marsh has shown that in the third cervical vertebra of *Ichthyornis* 'we catch nature in the act as it were' of modifying one form of vertebra into another, for this single vertebra in *Ichthyornis* is in vertical section 'moderately convex, while transversely it is strongly concave, thus presenting a near approach to the saddle-like articulation;' and he proceeds to point out that this specialised feature occurs at the first bend of the neck, and, greatly facilitating motion in a vertical plane, is 'mainly due originally to its predominance.' The form of the vertebræ would accordingly seem to be as much correlated with the mobility of the neck as is the form of the sternum with the faculty of flight. If, therefore, the development of the saddle shape be an indication of development, as well may be the outgrowth of a keel." In conclusion, the Professor observes that the question must be regarded as still unsettled, although his own opinion is strongly in favour of the Ratite being the earlier type.

On the other hand, Dr Gadow, in a communication of later date, concludes that the Ratitæ were most probably descendants of Birds which formerly possessed the power of flight; this view being said to be supported by the structure of the wings, and the nature of the feathers of the young.

In the following chapter a brief summary is given of the chief divisions of Birds, with mention of those families known to be represented in a fossil state. It would, however, exceed the limits of this work to give even the leading osteological characters of such families, since, owing to the great general similarity in the structure of all Carinate Birds, such characters could only be indicated by the introduction of a great mass of detail.

It should also be observed that the majority of writers rank the three primary divisions of Birds as subclasses, and the secondary divisions as orders, with the proviso that such orders are of very different value from those of Reptiles. With the object of avoiding this inequality the view of Professor Huxley, who has termed the primary divisions orders and the secondary ones suborders, has been followed in this work.

CHAPTER LVII.

CLASS AVES.

Orders Saururæ, Ratitæ, and Carinatæ.

Order I. Saururæ.—This extinct order is represented only by *Archæopteryx*, and may be characterised by the metacarpals being separate, and by the tail being longer than the body, and not terminating in a pygostyle.

Family Archæopterygidæ.—*Archæopteryx*, including birds of about the size of the common Rook, is found in the lithographic limestones of Solenhofen, near Pappenheim, in Bavaria, which are the representatives of the lower part of the English Kimeridge Clay. This genus was first made known by the impression of a single feather, to which the late Professor H. von Meyer gave the name *A. lithographica*. Subsequently the greater part of a skeleton, with impressions of the feathers of the wings and tail (fig. 1110), was obtained, which Sir R. Owen named *A. macrura;* while recently a second skeleton has been found which some writers regard as indicating a distinct species from the first. Of these two skeletons the former is preserved in the British and the latter in the Berlin Museum. Professor Carl Vogt, who first described the Berlin specimen, regarded *Archæopteryx* as a Reptile; but there can be no hesitation in classing it among the Birds. The jaws were furnished with teeth; the vertebræ were biconcave; and there was a well-ossified sternum, of considerable breadth, and probably provided with a carina. In the manus the three metacarpals remained distinct; and there were also three separate digits, each of which was terminated by a claw. In the pelvis the three component elements exhibit the Reptilian character of remaining distinct throughout life; and it is thought probable that the ischia united in a ventral symphysis. The distal portion of the fibula is placed in front of the tibia; and the metatarsals were either separate or but very imperfectly united together. The tail, again (fig. 1110),

differs from that of all other known Birds in that it consists of a series of long vertebræ, gradually tapering to the extremity, and each of which carries a pair of feathers. From the absence of impressions of feathers in the region of the body, it has been thought that only the wings and tail had these appendages; but it is far more probable that the feathers had fallen from the body as it lay on the old sea-shore, while those of the wings and tail still

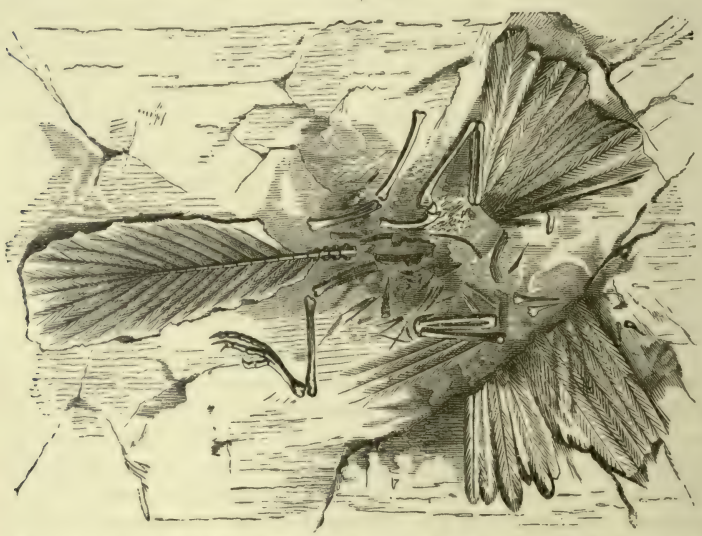


Fig. 1110.—Part of the skeleton, with impressions of the feathers of the wings and tail, of *Archæopteryx macrura*; from the lithographic limestone of Bavaria. Reduced.

adhered to their attachments. In the figure of the British Museum specimen of *A. macrura* (fig. 1110) the head is not shown; but it exists in an imperfect state of preservation in the slab. Till we know more of the other Birds of the Jurassic, the true relationship of *Archæopteryx* to existing forms cannot be determined.

Order II. Ratitæ.—The Ratitæ, or Struthious Birds, differ from the preceding order by the anchylosis of the metacarpals (when present) and the short tail, which may terminate in a pygostyle. They are further characterised by the sternum (figs. 1105, 1111) being devoid of a keel; by the long axes of the adjacent portions of the scapula and coracoid being approximately in the same line (fig. 1111), or at least forming an exceedingly obtuse angle at their junction; by the wings being useless for flight; and by the peculiar characters of the pelvis (figs. 1107, 1112), which have been already mentioned. There are, moreover,

important osteological characters connected with the palatal aspect of the skull which cannot be noticed here; and some other features have been mentioned in the preceding chapter. The massive bones are frequently filled with marrow. In all forms the fibula remains quite distinct from the tibia; and the distal end of the latter fre-

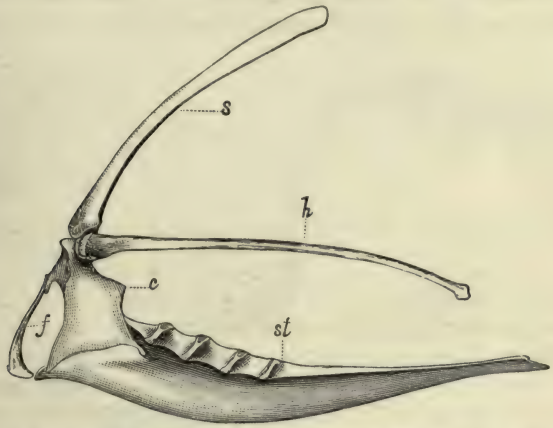


Fig. 1111.—Left half of the pectoral girdle and sternum of *Hesperornis regalis;* from the Cretaceous of North America. Reduced. *s*, Scapula; *h*, Humerus; *c*, Coracoid; *f*, Clavicle; *st*, Sternum. (After Marsh.)

quently has no bridge over the extensor tendons. In all existing forms the plumage presents the remarkable peculiarity that the barbs of the feathers, instead of being connected with one another by hooked barbules, as is usually the case, are remote and disconnected from one another, presenting some resemblance to hairs.

This order embraces the largest known members of the whole

Fig. 1112.—Left half of the pelvis of *Hesperornis regalis;* from the Cretaceous of North America. Reduced. Letters as in fig. 1107. (After Marsh.)

class; and from the scattered distribution of both its existing and fossil representatives is evidently an extremely ancient type. Its relations to the Carinatæ have been already alluded to in the preceding chapter. The order may be divided into two series, according to the presence or absence of teeth.

Toothed Series.—In this extinct series teeth are present in the jaws.

Suborder 1. Odontolcæ.—The type and only known representative of this suborder is *Hesperornis*, of the Cretaceous of North America. In this remarkable Bird (fig. 1113) the jaws (fig. 1117) were provided with a series of sharp-pointed teeth, sunk in a deep continuous groove; but the anterior portion of the upper jaw was

Fig. 1113.—Skeleton of *Hesperornis regalis*; from the Cretaceous of North America. About one-tenth natural size. (After Marsh.)

edentulous, and probably sheathed in a horny covering like that of existing Birds. Various parts of the skeleton are represented in figs. 1111, 1112, and 1117.

In its whole skeletal organisation *Hesperornis* conforms strictly to the existing Ratite type; but there were four digits in the pes (all of which were directed forwards), and Professor Marsh believes that it was of aquatic habits, and compares it to a swimming Ostrich. According to the description of the same authority, the tail consists of about twelve vertebræ, of which the last three or four are amalgamated to form a flat

terminal mass, there being at the same time clear indications that the tail was capable of an up and down movement in a vertical plane, thus probably fitting it to serve as a swimming-paddle or rudder. The vertebræ of the cervical and dorsal regions are of the ordinary ornithic type. The legs were powerfully constructed, and the feet were adapted to assist the bird in rapid motion through the water. The known remains of the typical *Hesperornis regalis* (fig. 1113) prove it to have been of larger dimensions than any of the aquatic members of the class with which we are acquainted at the present day. It appears to have stood between five and six feet high, and its inability to fly is fully compensated for by the numerous adaptations of its structure to a watery life. Its teeth prove it to have been carnivorous in its habits, and it probably lived upon fishes. A second species of this genus occurs in the same deposits, and is known as *Hesperornis crassipes;* but it was originally regarded as belonging to a distinct genus, and named *Lestornis.*

Toothless Series.—This series, which includes the whole of the remaining forms, is characterised by the absence of teeth.

Suborder 2. Æpyornithes.—This suborder is represented by a single family, the *Æpyornithidæ*, of the Pleistocene of Madagascar. The one known genus, *Æpyornis*, is characterised by the shortness of the beak; the small wings; the absence of a tibial bridge over the extensor tendons; and the presence of a hallux in the pes. The typical *Æ. maximus* appears to have attained dimensions rivalling those of the largest species of *Dinornis* (to be shortly mentioned); and eggs have been found in association with the bones measuring fourteen inches in diameter, and computed to be equal in capacity to three eggs of the Ostrich. At least two smaller species of the same genus occur in the Madagascar Pleistocene.

Suborder 3. Apteryges.—The members of the second suborder of this series are confined to New Zealand, and may all be included in the family *Apterygidæ*, which is now represented by the Kiwis or *Apteryx* (fig. 1114). They are distinguished from all other existing members of the order by their extremely long and slender beak, which is adapted for probing the soft marshy ground which they frequent in search of worms and other food. Omitting mention of the peculiar cranial and sacral characters, it may be observed that the wing has a comparatively short humerus, and not more than one ungual phalangeal. The tibia is furnished with a bony bridge over the extensor tendons; and there is a hallux to the pes. The feathers have no aftershafts. The Kiwis are essentially nocturnal in their habits. Remains of the existing species of *Apteryx* are found fossil in the Recent and Pleistocene deposits of New Zealand; while some much larger bones from the same deposits have been described by the late Sir Julius von Haast under the name of *Megalapteryx*, which appears to have been a giant form closely allied to the existing genus.

Suborder 4. Immanes.—This recently extinct group, like the last, is almost peculiar to New Zealand, and comprises some of the largest known Birds. The beak (fig. 1115) is short; the wings are either very small or totally wanting; the tibia has a distal bridge over the extensor tendons; and in some instances there was a hallux in the pes. The characters of the skull and pelvis come nearest to those of the next suborder, and the feathers have after-shafts. This group has been divided into the *Dinornithidæ* and *Palapterygidæ*, on account of the absence of the hallux in the former. Although this distinction has been doubted by some writers, who consider that *Dinornis* had a hallux, it appears to be

Fig. 1114.—*Apteryx australis*, New Zealand.

a valid one. Apart, however, from this point, according to the late Sir J. von Haast, the *Palapterygidæ* were provided with rudimentary wings, while in the *Dinornithidæ* those appendages were totally absent. Mr De Vis has described some bird-bones from the Pleistocene of Queensland under the name of *Dinornis queenslandiæ;* this being the only instance in which remains of this group have been recorded elsewhere than in New Zealand. Sir J. von Haast proposes to divide the *Palapterygidæ* into *Palapteryx* and *Euryapteryx*, and the *Dinornithidæ* into *Dinornis* and *Mionornis*.

The first evidence of the existence of this marvellous group was afforded by a fragment of the shaft of one of the bones of the leg brought to Sir

Richard Owen at a time when the existence of such huge Birds was totally unsuspected, and upon which evidence he founded the type genus. That the Moas, as these Birds are termed by the Maories of New Zealand, have only been exterminated at a comparatively recent date is proved by the occurrence of nearly entire skeletons with the skin and feathers still adhering to them, as well as by fragments of the eggs retaining their original pale-green colour. The largest species is *D. maximus*, of which the total height was about ten feet, the tibia measuring a yard in length. Another species, *D. elephantopus* (fig.

Fig. 1115.—Skeleton of *Dinornis elephantopus*; from the Pleistocene of New Zealand. Greatly reduced. (After Owen.)

1115), although not standing more than about six feet in height, was of even more massive construction, the toe-bones almost rivalling those of the elephant in size. The number of species described is very large.

Suborder 5. Megistanes.—The Emeus and Cassowaries are characterised by certain structural peculiarities in the base of the short cranium; by the moderately long humerus; the presence of only one complete digit in the manus, which is furnished with a claw; the absence of a ventral symphysis in the pubes or ischia;

the want of a bridge over the extensor tendons in the tibia; and the suppression of the hallux. The family *Dromœidæ* is represented by the existing Emeu (*Dromœus*) of Australia, and also by fossil species in the Pleistocene of the same country. *Dromornis*, from the latter deposits, is an extinct genus referable to this family. The characters of the pelvis of the existing genus are shown in fig. 1107. The *Casuariidæ*, now characteristic of the Australasian region, have not hitherto been definitely recorded in a fossil state; although it is possible that a phalangeal from the Indian Siwaliks may be referable to this family.

Suborder 6. Rheæ.—The *Rheidæ*, which alone constitute this group, and are confined to South America, differ from the Megistanes by the structure of the palate, as well as by the longer humerus, the presence of three digits (of which two are clawed) in the manus, by the ventral union of the ischia, and the absence of an aftershaft to the feathers. Remains of *Rhea*, which are referred to the existing species, occur in the Pleistocene cave-deposits of Brazil.

Suborder 7. Struthiones.—The family *Struthionidæ* is the sole representative of this suborder; the only existing species being the Ostrich (*Struthio camelus*), which is now confined to Africa and Arabia, although it formerly ranged into Persia, and probably also to Baluchistan and the north-west frontier of India. In addition to the characters of the palate, *Struthio* differs from *Rhea* by the union of the pubes in a ventral symphysis, and also by the suppression of the second digit of the pes, in consequence of which the distal end of the tarso-metatarsus has but two trochleæ. This genus is represented in the Pliocene Siwaliks of India, and also in the Lower Pliocene of the Isle of Samos, in the Turkish archipelago, by remains referred to two species. These forms, which may be specifically the same, appear closely allied to the existing Ostrich. An egg, from Tertiary beds near Gallipoli—the ancient Chersonese—described under the name of *Struthiolithus*, probably belongs to the existing genus, and very likely to the species occurring at Samos. These fossil forms point to the conclusion that the original home of the genus was probably in Asia.

Suborder 8. Gastornithes.—The *Gastornithidæ*, whose remains occur in the Lower Eocene of Europe, were large Birds which may probably be classed with the Ratitæ, and are apparently entitled to distinct subordinal rank. Their tibia agrees with that of the Apteryges and Immanes in having a bony bridge over the extensor tendons, but makes a curious approximation in shape to that of certain members of the Carinate suborder Anseres. The wings were somewhat larger than in the Ostrich; and the cranium, which is estimated to have been fifteen inches in length, had the alveolar margins of the jaws serrated, as in the genus *Odontopteryx* (fig.

1121). Remains of *Gastornis* have been recorded from Meudon, near Paris, from Rheims, and from Croydon, and have been referred to four species. The huge *Diatryma*, from the Lower Eocene of North America, appears to be closely allied to, if not identical with, *Gastornis*. Bird-bones from the Tertiary of South America, described by Dr Moreno under the name of *Mesembriornis*, and compared to the Anseres, probably indicate a member of this group, since they are fully as large as the corresponding bones of the Ostrich.

Here also may be noticed an imperfect cranium from the London Clay, described by Sir R. Owen as *Dasornis*, and regarded by him as pertaining to a Ratite Bird. And it may be also mentioned that an imperfect limb-bone from these deposits, which has been named *Megalornis*, may perhaps belong to the same genus.

Order III. Carinatæ.—The third order, which is now by far the most numerously represented, is generally characterised by the presence of a median keel to the sternum, and by the long axes of the adjacent portions of the scapula and coracoid forming at their junction an acute or slightly obtuse angle, as well as by the upward extension of the ischium towards the ilium (fig. 1102). In most cases the wings are adapted for flight, but in some instances they have become atrophied, while in others they are modified into swimming organs.

There is still considerable diversity of views obtaining among Ornithologists as to the classification of this order, and all such schemes must consequently be regarded as more or less provisional. In the present work the classification adopted by Mr P. L. Sclater is followed in the main, although certain modifications suggested by Professor Newton have been incorporated.

Before noticing those fossil forms which are susceptible of being placed in definite groups it will be advisable to mention briefly certain remains of which the affinity has not yet been determined, although it is probable that at least the majority should find a place in the present order. As to *Laopteryx*, of the Upper Jurassic of North America, there appears, as already mentioned, to be considerable doubt whether it is really Avian at all. In the Cretaceous of the same country we have *Apatornis*, *Graculavus*, *Laornis*, *Palæotringa*, and *Telmatornis*; many or all of which probably belong to the first suborder. In England the oldest known bird-remains occur in the Cambridge Greensand, and have been named *Enaliornis*, although it is quite probable that they may indicate more than one genus. Some of these vertebræ have more or less flattened centra; while the tarso-metatarsus, in which the fusion of the component elements is incomplete, is compared to that of the existing *Colymbus* and also to that of *Ichthyornis*, and it is highly prob-

able that these Birds were allied to the latter genus. The bones from the Cretaceous of Europe described as *Palæornis*, *Cimoliornis*, and *Cretornis*, belong to Ornithosauria.

In the Tertiary we have *Eupterornis* and *Remiornis* from the Lower Eocene of Rheims; while the Upper Eocene (Lower Oligo-

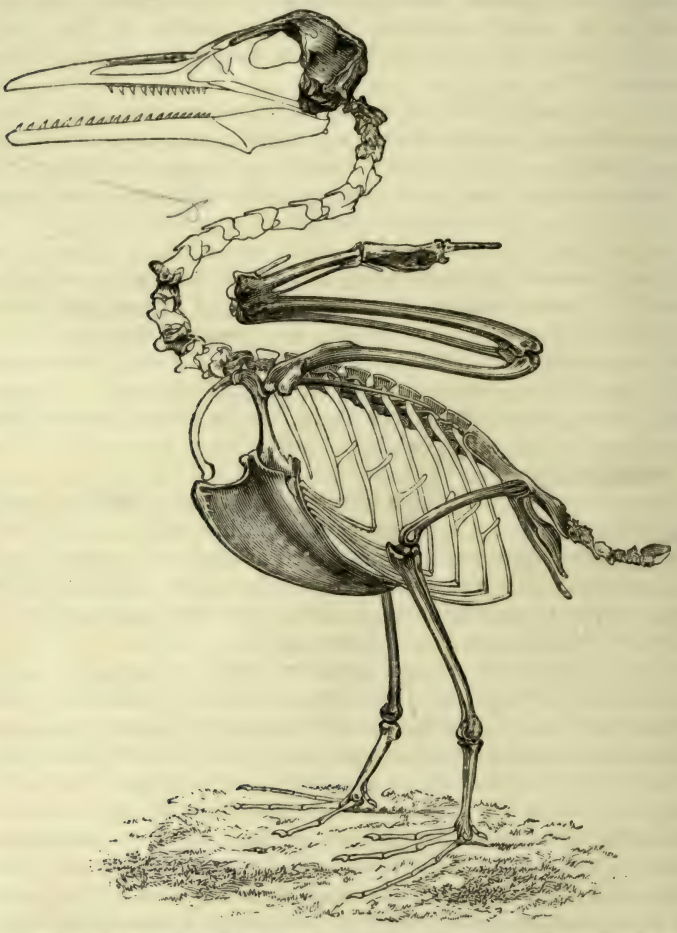


Fig. 1116.—Restoration of the skeleton of *Ichthyornis dispar;* from the Cretaceous of North America. Reduced. (After Marsh.)

cene) of Hampshire has yielded *Macrornis*, and the Lower Miocene (Upper Oligocene) of the same county *Ptenornis*.

Toothed Series.—This extinct series is characterised by the presence of teeth, and typically of amphicœlous vertebræ.

Suborder 1. Odontormæ.—The one suborder which is the only known representative of this series contains the family *Ichthyornithidæ*, from the North American Cretaceous, of which *Ichthyornis* is the only definitely known genus, although it is highly probable that *Apatornis*, and some of the other Cretaceous forms already mentioned, may also belong to this or an allied family. The teeth of *Ichthyornis* (fig. 1117, *a*) are comparatively large, and are set in distinct sockets; while the centra of the vertebræ are amphicœlous. There were about twenty teeth in each jaw, which are directed obliquely backwards. The rami of the mandible were but loosely united; and it is probable that the jaws were not sheathed in horn. The adult of the typical *I. dispar* (fig. 1116) was about equal in size to a Rock-pigeon; and in all essential features of its organisa-

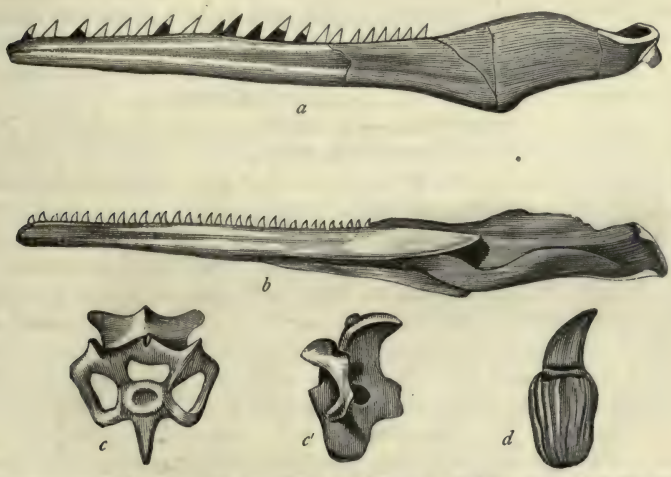


Fig. 1117.—*a*, Left ramus of the mandible of *Ichthyornis*, slightly enlarged; *b*, Do. of *Hesperornis*, about one-fourth natural size; *c*, *c'*, Anterior and lateral aspects of cervical vertebra of *Ichthyornis*, twice natural size; *d*, Tooth of *Hesperornis*, twice natural size. (After Marsh.)

tion this genus conforms so exactly with the existing Carinate type, that there appears every reason for including it in the same order, rather than following Professor Marsh's view of placing it, together with *Hesperornis*, in a separate order under the name of Odontornithes.

Toothless Series.—In this series, which comprises all existing Carinates, no teeth are ever functionally developed, although germs occur in the young of one group.

Suborder 2. Crypturi.—The Tinamous (*Tinamus*, &c.) which constitute this suborder, show more signs of affinity in the structure of their pelvis and skull to the Ratitæ, than is exhibited by any

other group of this order. They are confined to the New World, and are represented in a fossil state by remains of existing species of *Crypturus*, *Nothura*, *Tinamus*, and *Rhynchotus*, in the Pleistocene cave-deposits of Brazil.

Suborder 3. Impennes.—The Penguins (*Aptenodytes*, &c.) of the Antarctic regions form a peculiarly interesting and well-defined group of Birds, in which the wings are modified for swimming, and the component bones of the tarso-metatarsus are separated by vacuities. It has recently been proposed that the Impennes should form a primary group of equivalent rank with the Carinatæ, under the name of Eupodornithes. Unfortunately scarcely anything is known of their palæontological history, the only fossil type being *Palæeudyptes* from the Tertiary of New Zealand.

Suborder 4. Tubinares.—The Petrels, or *Procellariidæ*, are the only family of this group. The only known fossil representatives are members of the existing genus *Puffinus* (Shearwater), which have been recorded from the Lower Miocene of Allier, in France, and also from the Miocene of the United States.

Suborder 5. Pygopodes.—According to the opinion of Professor Newton this and the two following groups should be regarded merely as sections of a single suborder, but since no name has been proposed for this larger group the three divisions are retained. Of the Pygopodes, the *Alcidæ*, or Auks, include the Great Auk (*Alca impennis*) of the Arctic regions, which now appears to be totally extinct, but of which the remains are found abundantly in the peat and other superficial deposits of northern Europe. Remains referred to the genus *Uria* (Guillemots) are found in the Upper Pliocene of Italy; and Guillemots also occur in the Tertiary of the United States, where they have been described under the name of *Catarractes*. In the *Colymbidæ*, which includes the Grebes and Divers, remains of the Red-throated Diver (*Colymbus glacialis*) are found in the Pleistocene deposits of Mundesley, in Norfolk; while the extinct *Colymboides* of the Lower Miocene of Allier appears to be an allied form.

Suborder 6. Gaviæ.—Of the *Laridæ* (Gulls and Terns) a species of *Larus* occurs in the Allier Miocene; while *Hydrornis* of the latter deposits may probably be referred to the same family. An undetermined genus from the London Clay may perhaps be also referable to the present group.

Suborder 7. Limicolæ.—The Limicolæ are somewhat abundantly represented in Tertiary deposits; the subaquatic habits of many of its members being probably conducive to the preservation of their remains. In the family *Scolopacidæ* the genus *Numenius* (Curlew) is recorded from the Middle Miocene of Gers, in France, and the Pliocene of Italy; *Limosa* (Godwit) occurs in the Upper

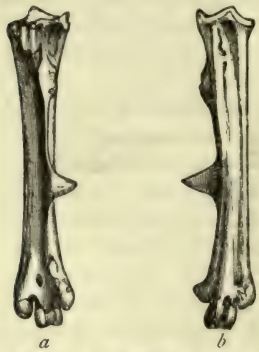
Eocene (Lower Oligocene) of Montmartre; *Totanus* (Redshank) in the Allier Miocene and the Pliocene of the Val d'Arno, in Tuscany; and *Tringa* (Knot and Dunlin) probably in the Montmartre, and certainly in the Allier beds, and the equivalent deposits of the Mayence basin. *Elorius* is an extinct genus from Allier, probably allied to *Limosa*. The Woodcock (*Scolopax rusticola*) has left its remains in the Pleistocene of Westphalia; and a species of *Himantopus* (Stilt) is found in the Allier Miocene. In the family *Charadriidæ* (Plovers) a species of the type genus *Charadrius* occurs in the Upper Eocene of Colorado; while the genus *Camascelus* (with which *Dolichopterus* is not improbably identical) is known from the Lower Miocene beds of Ronzon, in France.

Suborder 8. Alectorides.—The Alectorides form a somewhat ill-defined group, which is taken by Mr Sclater to include the *Otididæ*, although Professor Newton regards the latter as more nearly allied to the Gaviæ and Limicolæ. The family *Gruidæ*, or Cranes, is represented by the type genus *Grus* in the Pleistocene of Europe, India, and the United States, and also in the Lower Pliocene Pikermi beds of Greece, and the Miocene of Allier. Allied extinct genera are *Palæogrus* of the Eocene of Italy, and *Aletornis* of that of Wyoming. The *Otididæ* are represented by a species of Bustard (*Otis*) in the Allier Miocene.

Suborder 9. Fulicariæ.—This suborder comprises the Rails, Coots, Water-hens, etc.; all of which are included in the single family *Rallidæ*, and are of more or less aquatic habits. Birds referred to the type genus *Rallus* (Rail) occur in the Montmartre Eocene, the Miocene of Allier and Gers, and the Italian Pliocene. Remains of *Gallinula* (Water-hen) are recorded from the Pleistocene beds of Brazil and Queensland; in both of which deposits we meet with others referred to *Porphyrio* (Purple Water-hen)—a genus now widely distributed over the warmer regions of the globe. An extinct species of Coot (*Fulica*) has also been described from the Queensland Pleistocene. *Notornis*, which occurs in the Pleistocene of New Zealand and was also found living some years ago, is a large Rail allied to the Australian *Tribonyx*; while *Aptornis*, which is a very large form from the same deposits totally incapable of flight, is more nearly related to the existing *Ocydromus* of New Zealand. *Aphanapteryx* (*Erythromachus*) from the Pleistocene of Mauritius and Rodriguez is another large Rail allied to *Ocydromus*. Lastly, *Gypsornis*, of the Montmartre Eocene, is considered to be the earliest representative of this family.

Suborder 10. Gallinæ.—The Gallinæ form a large group of Birds mostly living to a considerable extent on the ground, and of comparatively stout build. They comprise the families *Megapodidæ* (Megapodes), *Cracidæ* (Curassows and Guans), *Phasianidæ*

(Pheasants, Turkeys, etc.), and *Tetraonidæ* (Grouse). The Gallinæ together with the following group of Columbæ were formerly bracketed together under the name of Rasores, and it is by no means certain that the departure from this arrangement is an advisable one. The skull (fig. 1103, p. 1210) has peculiar palatal features, a sharp curved beak, and a recurved process to the angle of the mandible. Many of the genera of Gallinæ (especially the males) are characterised by the presence of one or more strong bony spurs on the inner side of the tarso-metatarsus (fig. 1118). The first two families are at present unknown in a fossil condition. In the *Phasianidæ*, however, the typical genus *Phasianus* occurs in the Allier and Gers Miocene deposits, and also in the Lower Pliocene of Pikermi; *Francolinus* (Francolin) is represented by remains of existing species in the Pleistocene of Southern India (fig. 1118); *Coturnix* (Quail) in the Montmartre Eocene gypsum; the extinct *Palæortyx* in both the latter deposits and the Isère and Allier Miocene beds, the so-called *Palæoperdix* of the Mayence Miocene being probably identical; while a species of *Gallus*, somewhat larger than the existing Indian *G. Sonnerati*, is found in the Pikermi Pliocene. From the Miocene of the United States a Turkey (*Meleagris antiqua*) has been recorded, and is described as equal in size to the living species now characteristic of America. In the *Tetraonidæ* remains of the living Capercaillie (*Tetrao urogallus*) occur in the Norfolk Forest-bed; while an extinct species of the same genus has been described from the Upper Eocene of Languedoc. Remains of the existing Willow Grouse (*Lagopus albus*) are found in the Pleistocene of Westphalia.



a *b*

Fig. 1118.—*Francolinus pondicerianus*. The left tarso-metatarsus; from the Pleistocene of Madras. *a*, Posterior; *b*, Anterior aspect.

Suborder 11. Columbæ.—This group is taken to include the existing Sand-grouse (*Pteroclidæ*), and the Pigeons (*Columbidæ*). In the first-named family a species of the type genus *Pterocles* has been described from the Allier Miocene. The *Columbidæ* are known by a species referred to *Columba* from the last-named deposits, as well as by another provisionally referred to the same genus from the Pleistocene of Rodriguez. Of especial interest is a tarso-metatarsus from the Pleistocene of Queensland described by Mr De Vis under the name of *Progoura*, and regarded as indicating a bird allied to the Crowned-Pigeons (*Goura*) of New Guinea. *Goura* shows some signs of affinities to the *Phasianidæ*, and these resemblances are said to be more marked in *Progoura*, which is double the

size of the existing forms. Here also may be placed the now extinct family *Didida*, represented by the Dodo (*Didus ineptus*) of Mauritius, and the Solitaire (*Pezophaps solitaria*) of Rodriguez.

Of these two singular birds, the Dodo formerly inhabited Mauritius in great numbers, but the last record of its occurrence dates from the year 1681. It was a large and heavy bird (fig. 1119), bigger than a swan, and entirely unlike the pigeons in general appearance. The wings were rudimentary and completely useless as organs of flight. The legs were short and stout, the feet had four toes each, and the tail was extremely

Fig. 1119.—Skeleton of the Dodo (*Didus ineptus*), restored. (After Owen.

short, carrying, like the wings, a tuft of soft plumes. The beak (unlike that of any of the *Columbæ* except the little *Didunculus strigirostris*) was arched towards the end, and the upper jaw had a strongly-hooked apex, not unlike that of a bird of prey. The frontal region of the skull was greatly elevated and tumid, from the excessive development of cellular cavities between the two tables of the skull, and the actual brain-case was very small in proportion to the size of the cranium. In many respects allied to the Dodo, and, like it, incapable of flight, was the Solitaire, of which the last recorded appearance was in the year 1693. The Solitaire had longer legs and neck than the Dodo, the bill was less strongly arched, its forehead flatter, and there was developed

upon the radial side of the metacarpus an extraordinary spherical callus-like mass of bone, about as large as a musket-ball, and with a roughened surface. This singular callosity is much more developed in certain individuals—supposed to be males—than in others, which we may presume to be females; it was doubtless covered during life by a horny integument, and seems to have been used as an offensive weapon. Both these Birds are known to us by nearly entire skeletons obtained recently from the islands which they inhabited; and of the Dodo we have also a few remains belonging to entire specimens once preserved in our museums, which were unfortunately allowed to fall into decay, from apparent ignorance of their priceless value.

Remains of existing species of several genera of *Columbidæ* are found in the Pleistocene cave-deposits of Brazil.

Suborder 12. Anseres.—The Anseres, or Goose-like Birds, form a well-defined subordinal group, characterised by peculiar features, in the palatal region of the skull, and by the perfectly webbed feet; the beak being generally broad and spatulate, and the angle of the mandible with a recurved process (fig. 1120). All the existing members of this group are referred to the family *Anatidæ*, which is, however, split up into several subfamilies. A peculiar subfamily is represented by the living *Cereopsis*, of Australia; allied to which is the much larger extinct *Cnemiornis*, of the Pleistocene of New

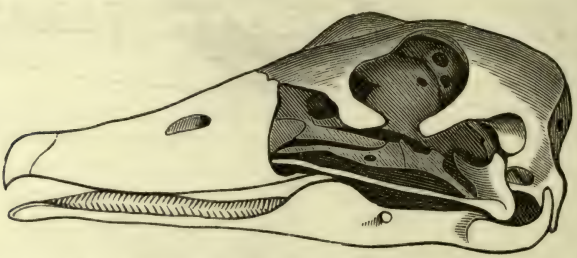


Fig 1120.—Skull of Spur-winged Goose (*Plectropterus gambensis*). Reduced.

Zealand, which was quite incapable of flight. In the subfamily *Anserinæ*, remains of the Grey-Lag Goose (*Anser cinereus*) occur in the European Pleistocene. The *Cygninæ*, or Swans, are represented by the extinct *Cygnus Falconeri*, from the Pleistocene cave-deposits of Malta. In the *Anatinæ* (Ducks) an extinct species of Tree-duck (*Dendrocygna*) is recorded from the Pleistocene of Queensland. Remains of the Wild-duck (*Anas boscas*) occur in the Pleistocene of Europe; *A. atavæ* and *A. cygniformis* are found in the Middle Miocene of Bavaria, the latter species being nearly as large as a Swan; *A. œningensis*, from the Upper Miocene of Switzerland; *A. lignifila*, from the Middle Miocene of Italy; and *A. Blanchardi*, from the Allier Miocene. Remains of the Shoveller

Duck (*Spatula clypeata*) have been found in the Norfolk Forest-bed. In the *Fuliguliné*, the type genus *Fuligula* (Pochard) is recorded from the Upper Pliocene of the Val d'Arno, in Italy, and *Nyroca* (White-eyed duck), from the Pleistocene of Queensland; while in the *Merginæ*, it is probable that *Mergus* (Merganser) was represented in the Pliocene Siwaliks of India. The extinct *Chenornis*, of the Italian Miocene, also belongs to this family, although its precise position is uncertain.

Suborder 13. Odontopteryges.—The *Odontopterygidæ*, represented by *Odontopteryx*, of the London Clay, appear to indicate a distinct subordinal group, which may be provisionally placed here. In this singular bird the alveolar margins of both jaws are furnished with tooth-like serrations (fig. 1121) which differ from true teeth in being actually parts of the osseous substance of the jaw itself, and thereby agree with those found in the Chelonian genera *Hardella* and *Batagur*. They are of triangular or compressed conical

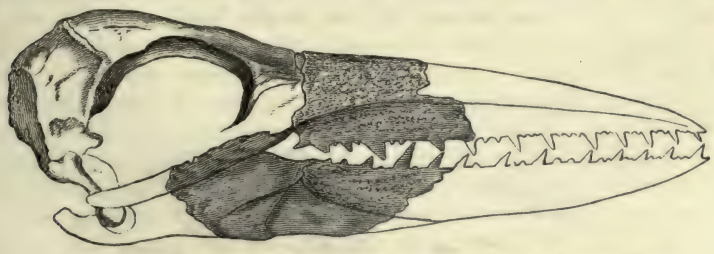


Fig. 1121.—Skull of *Odontopteryx toliapicus*, restored; from the London Clay. (After Owen.)

form, and of two sizes. Upon the whole, *Odontopteryx* would appear to be most nearly allied to the *Anatidæ*, but the serration of its jaws is an entirely unique character, unknown in any existing type.

Suborder 14. Palamedeæ.—Of this group, comprehending only the American Screamers (*Chauna*, &c.), no fossil representatives are known.

Suborder 15. Odontoglossæ.—The only family of this group is the *Phœnicopteridæ*, or Flamingos, which are exceedingly long-limbed waders, distinguished by a peculiar downward bend of the beak, and presenting characters connecting them on the one hand with the Anseres, and on the other with the Herodiones. The existing genus *Phœnicopterus* is found in the Allier Miocene; while in the same beds, as well as in the equivalent deposits of the Mayence basin, and also in the somewhat higher strata of Steinheim, in Bavaria, occurs the peculiar genus *Palælodus*, which, while apparently allied to *Phœnicopterus*, presents some affinity to

the Limicolæ, and also shows one osteological feature now only occurring among the *Pygopodes* in *Podiceps* (Grebes) and *Colymbus* (Divers). *Elornis*, from the Lower Miocene of Ronzon, appears to be also allied to the Flamingos; while *Agnopterus*, from the Upper Eocene of Montmartre, may perhaps be also included in the present group.

Suborder 16. Herodiones.—This suborder includes the *Plataleidæ*, or Spoonbills and Ibises; the *Ciconiidæ*, or Storks; and the *Ardeidæ*, or Herons; all of which are waders. The *Plataleidæ* are represented in past epochs by an extinct species of *Ibis* (*I. pagana*), from the Allier and Steinheim Miocene; while the existing Asiatic Black-headed Ibis (*I. melanocephala*) has left its remains (fig. 1108, p. 1217) in the Pleistocene cave-deposits of southern India. Another existing species of this genus occurs in the cave-deposits of Brazil. In the *Ciconiidæ*, an extinct species of the African and Oriental genus *Leptoptilus* (*Argala*), which includes the giant Adjutant Stork of India, is found in the Pliocene Siwaliks of the latter country, and another in the Middle Miocene of Bavaria; while an undetermined Ciconioid, from the Pikermi beds of Attica, may possibly belong to the same genus. Part of a metatarsus, from the Tertiary of Argentina, indicates a bird double the size of the Pampean Stork, and has been made the type of the genus *Palæociconia*. The Indian Siwaliks have also yielded remains of another giant Stork, of which the genus has not yet been determined. In the Pleistocene of Queensland there occurs an extinct species of *Xenorhynchus*. In the *Ardeidæ* the type genus *Ardea* (Heron) is represented in the Bavarian Miocene by a species (*A. similis*) apparently closely allied to, but rather stouter than, the common Heron (*A. cinerea*); and remains of the same genus also occur in the Miocene of Allier and Gers. The Night-Herons (*Nycticorax*) are known by an extinct species in the Pleistocene deposits of the Island of Rodriguez. Finally, certain remains from the London Clay may possibly indicate that this family dates from that epoch.

Suborder 17. Steganopodes.—In the Steganopodes are included a number of web-footed Birds, such as the Darters (*Plotidæ*), Cormorants (*Phalacrocoracidæ*), Albatrosses and Frigate-Birds (*Fregatidæ*), and the Pelicans (*Pelicanidæ*), some of which are regarded as more or less closely allied to the Gaviæ, while it is suggested that there may also be a connection between this group and the Accipitres. The *Plotidæ* are only known in a fossil state by a species of the one genus *Plotus*, from the Pleistocene of Queensland. In the *Phalacrocoracidæ* we find the type genus *Phalacrocorax* (*Graculus* or *Cormoranus*) in the Eocene of Montmartre, the Allier Miocene, the Pliocene of the United States, and prob-

ably also in the Indian Siwaliks; remains of the existing Cormorant (*P. carbo*) being found in the Norfolk Forest-bed. *Sula* (Gannet) occurs in the Miocene beds of Colorado and of Ronzon (Puy-en-Velay); while *Pelagornis*, of the Allier Miocene, is provisionally placed in this family. In the *Fregatidæ* remains of a *Diomedia*, apparently closely allied to the Albatrosses of the Southern seas, have been described from beds at the top of the Suffolk Crag; while it is considered probable that *Argillornis*, of the London Clay, indicates the existence of this family in the Lower Eocene. In the *Pelecanidæ* remains of true Pelicans (*Pelecanus*) occur in the Miocene of Allier and Bavaria, as well as in the Indian Siwaliks.

Suborder 18. Accipitres.—The Accipitres, or Diurnal Birds of Prey, are characterised by their curved beak (fig. 1122, B), the absence of a circle of feathers round the eye, and the powerful talons of the foot (fig. 1122, A), as well as by many osteological features, and especially the nearly straight line formed by the three

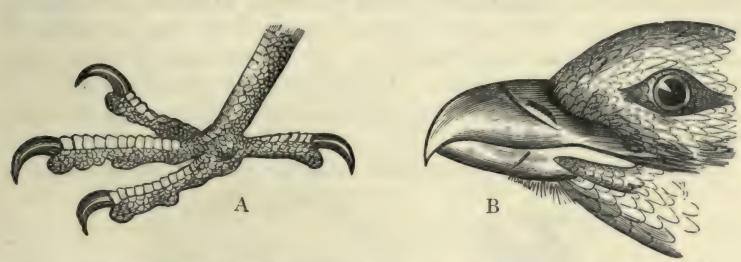


Fig. 1122.—A, Foot of the Peregrine Falcon; B, Head of Buzzard. Reduced.

terminal trochleæ of the tarso-metatarsus (fig. 1123), and the absence of a bony bridge over the extensor tendons at the distal extremity of the tibia. The probability of this group being related to the Steganopodes has been already noticed. The *Cathartidæ*, or American Vultures, are represented by existing species of *Cathartes* and *Gyparchus* in the Pleistocene of the Brazilian caves. It has also been considered that this group is represented in Europe by *Lithornis vulturinus*, of the London Clay; an opinion which, if confirmed, will be of considerable interest from a distributional point of view. The peculiar *Serpentariidæ*, or Secretary Vultures, of Africa, are known by a species of the one existing genus *Serpentarius* from the Allier Miocene. The *Falconidæ* include all the remaining genera, which are grouped in several subfamilies. Of these the *Vulturinæ*, or true Vultures, are represented in the Pleistocene breccia of Sardinia by remains of the type genus *Vultur;* while those of the existing Afro-Indian *Neophron percnopterus* are

recorded from the equivalent cave-deposits of southern India. In the other groups we have evidence of a species of either *Milvus* or *Circus* (fig. 1123) from the last-named deposits, the figure being given in order to show the form of the distal end of the tarso-metatarsus so characteristic of this suborder. *Milvus* is recorded from the Allier Miocene; and *Falco* from the Montmartre Eocene. Species referred to *Aquila* are mentioned both from the Miocene of Allier and Gers, and the Sardinian Pleistocene; while *Haliaëtus* is recorded from Gers. Of extinct genera *Palæohierax*, from the Allier Miocene, is regarded as being allied to *Aquila;* while *Palæocircus*, of the Montmartre Eocene, is described as showing affinity to the Buzzards (*Buteo*), and the Osprey (*Pandion*); *Teracus*, from the Ronzon Miocene, being an imperfectly known form. The largest known member of this suborder is *Harpagornis*, from the Pleistocene of New Zealand, which was apparently allied to *Circus*. Finally, several existing species of *Falconidæ* are recorded from the Pleistocene of the Brazilian caves.

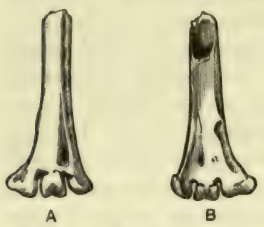


Fig. 1123.—(?) *Milvus* or *Circus*, sp. The distal half of the left tarso-metatarsus, from the anterior (A) and posterior (B) aspects; from the Pleistocene of Madras

SUBORDER 19. STRIGES.—The Striges, or Owls, were formerly

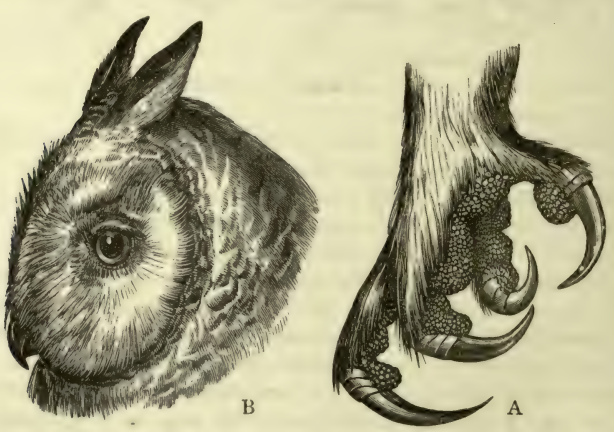


Fig. 1124.—A, Foot of the Long-eared Owl (*Otus vulgaris*); B, Head of the same. Reduced.

grouped with the Accipitres, but are now regarded as being probably more nearly allied to the Parrots. Comparatively few fossil forms are known; but in the *Asionidæ*, or Eagle-Owls, we have the

great Eagle-Owl (*Bubo ignavus*) in the Norfolk Forest-bed, and the existing Indian *B. coromandus* in the Pleistocene of Madras; while this genus is also recorded from the Allier Miocene, and is represented in the Eocene of the United States by *B. leptosteus*, which was about two-thirds the size of the existing *B. virginianus* now inhabiting the same regions. The existing Ceylon Fish-Owl (*Cetupa*[1] *ceylonensis*) occurs in the Pleistocene of Madras, and the great European Snowy Owl (*Nyctea scandiaca*) in that of Westphalia. In the *Strigidæ*, or true Owls, remains of an extinct species of *Carine* have been described from the Pleistocene of the Island of Rodriguez; while bones from the Miocene of Allier and Gers have been referred to *Strix*.

Suborder 20. Psittaci.—The Parrots, Cockatoos, and their allies, which constitute this suborder, are now confined to the warmer regions of the globe, and are remarkable for the presence of a hinge-joint at the base of the strongly-curved cranial portion of the beak, whereby the upper jaw can be moved upon the cranium proper, as is shown in fig. 1125, A. All the genera are of scansorial

Fig. 1125.—Right lateral aspect of the skull (A) and of the left pes (B) of *Psittacus erythacus*. Reduced. *a*, First (hallux); *b*, Second; *c*, Third; *d*, Fourth digit. (After Blanchard.)

habits, and the foot has a hallux (fig. 1125, B). In the *Psittacidæ*, or true Parrots, remains from the Allier Miocene have been referred to the typical African genus *Psittacus*, but that term must be used in a wider sense than the one in which it is employed by the students of recent Ornithology. *Lophopsittacus* is an extinct genus from the Pleistocene of Rodriguez. Remains of the genus *Nestor*, peculiar to New Zealand, occur in the deposits of that country which yield *Dinornis*, and probably belong to existing species. The American Macaws are represented by species of *Ara* in the Brazilian cave-deposits. In the *Palæornithidæ*, which includes the Lories and Parakeets, an extinct species of the existing African and Oriental genus *Palæornis* occurs in the Pleistocene of Rodriguez, which has also yielded the extinct *Necropsittacus*. The *Stringopidæ* of New

[1] Amended from *Ketupa*.

Zealand, and the *Cacatuidæ* (Cockatoos) of Australia, have not yet been recorded in a fossil state.

Suborder 21. Picariæ.—The *Picariæ* are a somewhat heterogeneous group of Birds, of which it will be unnecessary to mention all the families, since only a few are definitely in a fossil condition. To the African *Musophagidæ*, or Plaintain-cutters, it is thought the extinct *Necrornis*, from the Miocene of Gers, may possibly belong. The remarkable *Leptosomatidæ*, of Madagascar, which connect the *Coraciidæ* with the *Cuculidæ*, are represented by a species of the type genus *Leptosoma* in the Allier Miocene. The latter deposits have also yielded a species of *Trogon*, the type of the family *Trogonidæ*. *Limnatornis*, of the same beds, is referred to the *Upupidæ*, or Hoopoes; while it is considered that the Upper Eocene *Cryptornis* may belong to the *Bucerotidæ*, or Hornbills, of the Ethiopian and Oriental regions. The *Alcedinidæ*, or King-fishers, are represented in the London Clay by *Halcyornis;* while in the *Picidæ* (Woodpeckers) we have the existing genus *Picus* in the Middle Miocene of Isère and the Lower Miocene of Allier, and the extinct *Uintornis* in the Eocene of Wyoming. Finally, the *Cypselidæ*, or Swifts, are known to have existed since the Allier Miocene, where we find a species of the type genus *Cypselus* closely allied to existing forms.

Suborder 22. Passeres.—Of the Passeres, the last and most highly organised group of the class, an enormous number of living genera and species are known; but from the comparatively small size of the majority of species, and the difficulty of distinguishing even genera by fragmentary bones, scarcely anything is known of their palæontological history. To the *Alaudidæ* (Larks) has been provisionally referred *Protornis*, from the Lower Eocene of Glarus in Switzerland; and *Alauda* is recorded from the Upper Pliocene of Italy. In the *Corvidæ* (Crows) the type genus *Corvus* has been described from the Allier Miocene. In the Pleistocene of Rodriguez the extinct *Necropsar* is a Starling (*Sturnidæ*) closely allied to the pied and crested *Fregilopus* of Reunion, which also appears to have recently become extinct. Among the *Fringillidæ* (Finches) *Loxia* and *Passer* are provisionally recorded from the Allier Miocene; and to this family may perhaps be referred the extinct genus *Palæospiza*, from the Upper Eocene of Colorado. Finally, we have a representative of the *Laniidæ*, or Shrikes, in a species of *Lanius* from the Allier Miocene; while the *Sittidæ* (Nuthatches) date their existence at least from the fossil *Sitta* of the Montmartre Eocene, and are also represented by a species in the Upper Pliocene of Italy. Lastly, the cave-deposits of Brazil have yielded remains of several existing forms of Passerines, among which it will suffice to mention a species of Swallow (*Hirundo*).

LITERATURE OF AVES.

1. DAMES (W. B.)—"Ueber *Archæopteryx*." 'Pal. Abhandl.,' vol. ii., art. 3 (1884).
2. DAVIES (W.)—"On some Fossil Bird-Remains from the Siwalik Hills." 'Geological Magazine,' dec. ii., vol. vii. (1880).
3. EDWARDS (A. MILNE-).—"Récherches Anatomiques et Paléontologiques pour servir à l'histoire des Oiseaux fossiles de la France." Paris (1867-77).
4. GÜNTHER (A.), and NEWTON (E.)—"The Extinct Birds of Rodriguez." 'Transit of Venus Expedition.'
5. HAAST (J. VON).—"On *Harpagornis*, an Extinct Genus of gigantic Raptorial Birds of New Zealand." 'Trans. New Zealand Institute,' 1874.
6. —— "On *Megalapteryx Hectori*, a new Gigantic Species of Apterygian Bird." 'Trans. Zool. Soc.,' vol. xii. (1886).
7. HUXLEY (T. H.)—"On the Classification of Birds." 'Proc. Zool. Soc.' 1867.
8. LEMOINE (V.)—"Récherches sur les Oiseaux Fossiles des Terrains Tertiaires des Environs de Reims," parts 1 and 2. Rheims (1878-81).
9. LYDEKKER (R.)—"Siwalik Birds." 'Palæontologia Indica' (Mem. 'Geol. Surv. Ind.'), ser. 10, vol. iii., part 4 (1884).
10. MARSH (O. C.)—"Odontornithes: A Monograph of the Extinct Toothed Birds of North America." Washington (1880).
11. —— "Discovery of a Fossil Bird in the Jurassic of Wyoming." 'American Journal of Science,' ser. 3, vol. xxi. (1881).
12. NEWTON (A.)—"Ornithology." 'Encyclopædia Britannica,' 9th ed.
13. —— and (E.)—"Osteology of the Solitaire or Didine Bird of the Island of Rodriguez." 'Phil. Trans.' 1869.
14. —— (E.), and CLARK (J. W.)—"On the Osteology of the Solitaire (*Pezophaps solitaria*, Gmel)." 'Transit of Venus Expedition.'
15. —— (A.) and PARKER (W. K.)—"Birds." 'Encyclopædia Britannica,' 9th ed. (1875).
16. OWEN (R.)—"*Archæopteryx macrura*." 'Phil. Trans.' 1863.
17. —— "Memoir on the Dodo." 1866.
18. —— "Memoir on the Extinct Wingless Birds of New Zealand." London (1878).
19. —— "On *Argillornis longipennis*, Owen, a large Bird of Flight, from the Eocene Clay of Sheppey." 'Quart. Journ. Geol. Soc.,' vol. xxxvi. (1880).
20. —— "On the Skull of a Dentigerous Bird from the London Clay of Sheppey." 'Quart. Journ. Geol. Soc.,' vol. xxix. (1873).
21. —— "On Dinornis." 'Trans. Zool. Soc.' 1839-85.
22. —— "Osteology of the Dodo." 'Trans. Zool. Soc.' 1867.
23. PORTIS (A.)—"Contribuzioni alla Ornitologia Italiana," part 2. 'Mem. Ac. R. Torino,' ser. 2, vol. xxxviii. (1887).
24. SEELEY (H. G.)—"On the British Fossil Cretaceous Birds." 'Quart. Journ. Geol. Soc.,' vol. xxxii. (1876).
25. STRICKLAND (H. E.) and MELVILLE (A. G.)—"The Dodo and its Kindred." London (1848).

26. VIS (C. W. DE).—"A Glimpse of the Post-tertiary Avifauna of Queensland." 'Proc. Linn. Soc. N. South Wales,' vol. iii. (1888).
27. VOGT (C.)—"L' *Archæopteryx macrura*—Un Intermédiare entre les Oiseaux et les Reptiles." 'Rev. Sci. France et l'Etranger,' vol. ix. (1879). Translated in the 'Ibis' for 1880.
28. WINGE (O.)—"Fugle fra Knoglehaler i Brasilien" (Birds from the Brazilian Bone-Caves). 'Museo Lundii' (1887).
29. WOODWARD (H.)—"On Flightless Birds." 'Proc. Geologists' Association,' vol. ix. (1886).

CHAPTER LVIII.

CLASS MAMMALIA.

GENERAL STRUCTURE.

THE Mammalia, or highest class of the Vertebrata, are characterised by having some part of the integument provided with hairs at some period of life, and by the young being nourished for a longer or shorter time by the milk, or special secretion of the mammary glands. As characters available in the case of fossils, it may be observed that the cranium articulates with the atlas vertebra by two occipital condyles, mainly formed by the exoccipitals; while each ramus of the mandible consists of only a single piece, which proximally articulates directly with the squamosal element of the cranium without the intervention of a quadrate; and there is no movable joint between the proximal and distal rows of the tarsus. Like the Sauropsida, Mammals possess during development an amnion and allantois, and are totally devoid of gills. They differ from Reptiles and agree with Birds in having a four-chambered heart, warm blood, and a complete double circulation. They are peculiar in that the red corpuscles of the blood are not nucleated and usually circular; in the lungs being freely suspended in the thoracic cavity, which is separated from the abdomen by a muscular partition termed the *diaphragm;* in the presence of only the left aortic arch; and in the perfection of the transverse commissure (corpus callosum) connecting the two cerebral hemispheres. Feathers, moreover, are never present, and there is no *syrinx* or lower vocal organ, although a complete *larynx* is always developed in the upper portion of the *trachea*, or respiratory tube.

It will be unnecessary in this work to make any further mention of the soft parts, but a few remarks must be made concerning the tegumentary and dental systems, and the endoskeleton; although the student must refer to other works for fuller information on these subjects. With regard to the tegumentary system, it will suffice to

observe that imbricated horny scales occur in the epidermis only in the family *Manidæ* among the Edentata; and flat horny shields, with their edges in apposition, in the tails of the Beaver, Rats, and certain Insectivores and Marsupials. The Armadillos and Glyptodonts develop, however, a series of bony scutes articulating with one another in the true dermis, which are covered by horny epidermal shields; the whole structure being thus precisely comparable to that obtaining in the Crocodilia. Smaller separate bony scutes also occur in the dermis of *Mylodon*. The horns of the Ruminants and Rhinoceroses are entirely epidermal structures; the former being hollow sheaths enveloping bony cores, while the latter are solid throughout.

The dental system, as being of extreme importance for the determination of the extinct forms, must be noticed somewhat more fully. Calcified teeth are developed in the great majority of Mammals, but in the true Whales they occur only in the embryo, in *Ornithorhynchus* they disappear in the adult, while in *Echidna*, *Manis*, and *Myrmecophaga*, no traces of them have as yet been detected. In the adult of *Ornithorhynchus* and *Rhytina* the function of teeth is discharged by horny plates, or *cornules* on the palate. In all other forms, however, true teeth, which are developed only in the premaxilla, maxilla, and dentary bones, are present; and are usually composed of the three elements, dentine, enamel, and cement, although occasionally, as in the existing Edentates, the enamel is absent. The dentine, or ivory, forms the chief constituent of most teeth. This is coated, either completely or partially, in the majority of cases by a thin investing layer of the hard flint-like enamel, which is readily distinguished from the dentine by its bluish-white and translucent appearance, while the outermost coat of cement, when present, is of a dull opaque white, or buff, colour. The cement is frequently found only as a thin coating at the roots of the teeth; but it is very largely developed in the crowns of the hinder teeth of many Ungulates. In the teeth of the great majority of Mammals (as in fig. 1126) the crown, or exposed portion, is sharply defined by a construction known as the *neck* from the root, or embedded portion; but in those teeth to be immediately noticed, which grow continuously, there is no such distinction between the crown and the root. In no Mammals are the teeth anchylosed to the bones of the jaw;[1] and they are invariably implanted in distinct alveoli, or sockets, which are, however, very imperfect in certain Cetacea. In all young animals, while the teeth are still growing, the inferior extremity of the root, or roots, is widely open; but in the majority of instances this aperture becomes completely closed in the adult (fig. 1126). In certain

[1] Except, perhaps, the incisors of the Shrews.

cases, however, as in the anterior cutting-teeth of the Rodents and the tusks of the Elephant, the root remains permanently open below, and the tooth consequently continues to grow throughout the life of the animal. In such circumstances the teeth are said to have persistent pulps. The anterior teeth (fig. 1126, *c*, *i*), with some rare exceptions, are of simple structure and have but a single root; but the hinder ones (*ibid.*, *pm*, *m*) very generally have more or less complex crowns, which may be supported by from two to four roots; such division of the roots being unknown outside the Mammalian class. In many forms the summits or sides of the crowns of the hinder teeth may be interpenetrated by deep re-entering folds of enamel, which may be filled up with cement; these folds being espe-

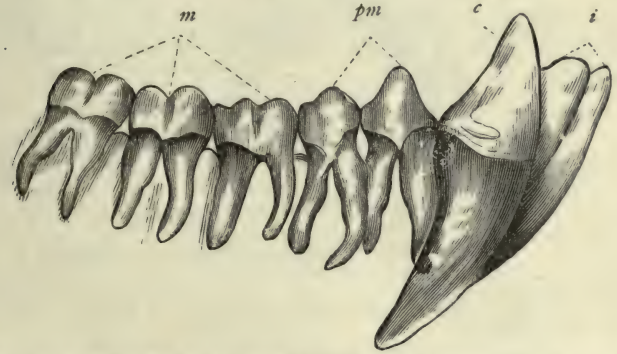


Fig. 1126.—Teeth of the right side of the lower jaw of the Chimpanzee. *i*, Incisors; *c*, Canine; *pm*, Premolars; *m*, True molars. (After Owen.)

cially developed in many Rodents and Ungulates. From this structure it will naturally result that when a horizontal section of the crown of such a tooth is made by the wearing of the upper against the lower series, an extremely complex pattern will appear, as will be seen in the figures of the cheek-teeth of the above-mentioned groups which are given below. Much more rarely, as in the Horse, there may be an infolding of the enamel in the summits of the crowns of the anterior teeth.

With the exception of the above-mentioned edentulous forms, in all existing Mammals one definite set of teeth, which is almost always constant in number, is developed, and this set when it appears usually persists throughout the remaining portion of the life of its owner. In a large number of species this is the only set ever developed; and such species, or groups of species, are consequently said to be *Monophyodont*. In the greater majority of Mammals, however, the development of occasionally only one, but usually of the greater number of the anterior teeth of this permanent set is

retarded, and their function filled for a time by an earlier series of so-called milk-teeth; such Mammals being accordingly termed *Diphyodont.* As development proceeds the permanent teeth in such Mammals come up beneath the milk-teeth, and thus replace them in a vertical direction; but there are instances where certain of these milk-teeth have no such permanent successors, while in other cases the anterior teeth which come into use with the permanent dentition have no milk predecessors. Those Mammals with a Mono-

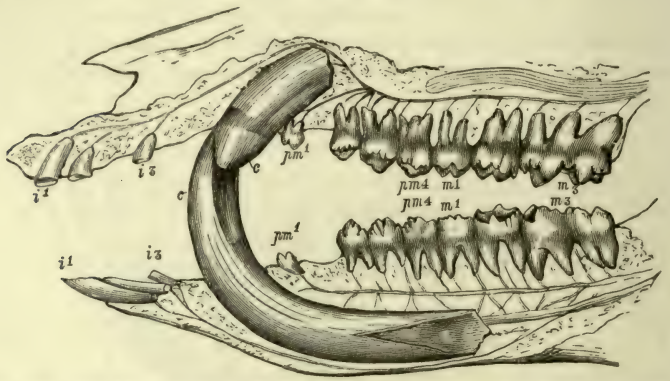


Fig. 1127.—Outer lateral aspect of the left dentition of the Pig (*Sus scrofa*), with the outer lamina of bone removed, in order to exhibit the roots of the teeth. *i*, Incisors; *c*, Canine; *pm*, Premolars; *m*, True molars.

phyodont dentition present the least specialised development, since the milk-series appears from the latest researches to be an addition grafted on to the permanent one; and there is accordingly no homology between this definite single replacement and the irregular continuous change which takes place in many Reptiles. In some Mammals, like the Dolphins (*Delphinidæ*), all the teeth are so much alike that they cannot be divided into groups, and the dentition is then described as *Homœodont;* but in the majority the permanent teeth, either from their position or their mode of succession, can be separated into four distinct groups (as in figs. 1126, 1127), and the dentition is then termed *Heterodont.* In Eutherian Diphyodont Mammals the total number of teeth of the permanent series does not normally exceed 44; and in forms like *Sus* (fig. 1127), or the extinct *Anoplotherium*, where this full complement is present, the first three upper teeth (*i* 1-*i* 3) on either side, which are situated in the premaxillæ, are termed *incisors;* the last three (*m* 1-*m* 3), which are distinguished by having no milk-predecessors, *true molars;* the four submolariform teeth (*pm* 1-*pm* 4) in advance of the latter, of which the last three have such deciduous predecessors, *premolars;* and

the single subconical tooth (*c*) situated between the premolars and the incisors the *canine;* the latter tooth being the first of those borne by the maxilla. The same terms are applied to the corresponding lower teeth, although it will be unnecessary here to indicate how such serial correspondence is worked out. For the sake of brevity such a dentition may be expressed by the numerical formula — $I.\ \frac{3—3}{3—3}$; $C.\ \frac{1—1}{1—1}$; $Pm.\ \frac{4—4}{4—4}$; $M.\ \frac{3—3}{3—3} = 44$; but since the teeth of opposite sides of the jaws always correspond, such a formula may be further simplified into—

$$I.\ \frac{3}{3};\ C.\ \frac{1}{1};\ Pm.\ \frac{4}{4};\ M.\ \frac{3}{3} = 22 \times 2 = 44.$$

The individual teeth of each group are enumerated from before backwards, and by such a formula as the following—viz.,

$$\frac{I.\ 1,\ I.\ 2,\ I.\ 3,\ C.,\ Pm.\ 1,\ Pm.\ 2,\ Pm.\ 3,\ Pm.\ 4,\ M.\ 1,\ M.\ 2,\ M.\ 3,}{I.\ 1,\ I.\ 2,\ I.\ 3,\ C.,\ Pm.\ 1,\ Pm.\ 2,\ Pm.\ 3,\ Pm.\ 4,\ M.\ 1,\ M.\ 2,\ M.\ 3,}$$

—each individual tooth can be specially noted. Thus, for example, *pm.* 1 will indicate the first upper premolar, and *m.* 3 the third, or last, lower true molar. It will frequently, moreover, be convenient to speak of the incisors and the canine collectively as the *cutting-*, and of the premolars and true molars as the *cheek-teeth.* It is very generally the case that when the true molars are reduced to less than three it is the hinder tooth, or teeth, that disappear; in the premolars it is, however, frequently the anterior teeth that are wanting, although this is by no means invariably the case, and there are instances known where the second and fourth disappear, while the first and third remain. In the figure of the lower dentition of the Chimpanzee given on page 1247, the two premolars are usually reckoned as *pm.* 3 and *pm.* 4, but it is not certain that such is really the case. Again, it has been suggested that the two incisors found in that species, in common with other Primates, may be the first and third of the typical Eutherian series of three, although other authorities regard them as the second and third. It may also be observed that in some groups, as the Carnivora, the specialised forms tend to lose the molars and retain the full number of anterior teeth; while in others, like the Ungulates, the reverse condition obtains.

The milk-dentition may be expressed by a similar formula with the prefix of the letter *M.* to the symbols. The typical milk-series will thus be written as $M.i.\ \frac{3}{3}$, $M.\ c\frac{1}{1}$, $M.m.\ \frac{3}{3}$; the three milk-molars corresponding to the last three premolars of the permanent series. In a few Ungulates, however, such as *Tapirus*, and sometimes *Rhinoceros* and *Palæotherium*, four milk-molars are developed.

Among the existing Metatheria the number of true molars is generally $\frac{4}{4}$, while the premolars are very frequently reduced in number, and there may be five upper incisors. In one existing, and several Mesozoic members of that subclass, the number of true molars exceeds four; but, with the possible exception of some of these extinct types, there is no known instance of a heterodont Mammal normally having more than four premolars; and there is never more than a single canine tooth on either side of each jaw.

Since in Ungulates it is sometimes difficult to distinguish molars from premolars, it may be well to mention how the division between the two series can always be determined. Since the first tooth of the true molar series always comes into use before the last milk-molar is shed, it is obvious that in the adult the first true molar will always be more worn than the last premolar. Thus, in the three teeth of *Hipparion* represented in fig. 1233, the tooth on the left side of the figure being more worn than the one in the middle is thereby shown to be the first of the true molar series; the other two being consequently premolars.

The different types of cheek-teeth will be mentioned under the head of the various orders and families, but a few general observations may be recorded here. Professor Osborn considers that the primitive Mammals had simple conical teeth with undivided fangs, and that the crowns of the teeth of the upper and lower jaws mutually interlocked. Teeth nearly approaching to this type occur in the Triassic *Dromatherium* (fig. 1140), while those of the Dolphins are looked upon as a reversion to this type. Another simple type, according to the views of the same author, is that found in *Triconodon* and *Priacodon* (fig. 1147), where the upper and lower teeth alike consist of three cusps in a line; the upper teeth biting on the outer side of the lower. A third common, and apparently very generalised, type of tooth is that known as the *tritubercular*. This consists in the upper teeth of one inner and two outer cusps, arranged in a triangle; while in the lower jaw the reverse arrangement obtains, so that there is one cusp on the outer and two cusps on the inner side of the crown. An example of this type of structure in its simplest form occurs in the Mesozoic genus *Spalacotherium*. Modifications of this type occur in the lower teeth of many Marsupials (*e.g.*, fig. 1145), and also in the lower carnassial teeth of the Carnivora, of which mention is made in the sequel. The tritubercular type of tooth is regarded by the American Palæontologists as one which has given rise to a large number of the more complex modifications; and it is extremely common among the generalised Mammals of the Lower Eocene.

In adult Mammals, as in the Sauropsida, the whole of the primitive cartilaginous cranium is replaced by extensive ossifications, except in the ethmoidal region; and these bones, with the exception of those of the mandible, hyoid arch, and internal auditory apparatus, are similarly articulated together at their edges by suture. As age goes on there is generally a tendency to the obliteration of these sutures, this being most marked in *Manis*. In all cases the parasphenoid has ceased to exist as a distinct ossification. It has already been observed that the hinder part of the cranium articulates with the first, or atlas, vertebra by two exoccipital condyles, and also that each of the two rami of the mandible is composed of a single bone articulating at its proximal or hinder extremity with the squamosal of the cranium. Owing to the complete incorporation of the squamosal and parietal in the walls of the brain-case there is (as in the Birds) no superior temporal arcade; but an inferior, or zygomatic, arcade is nearly always present; and, as in Crocodiles (although not in Birds), forms the lower border of the orbit. This inferior temporal arcade, or arch, differs, however, from that of most Sauropsida in that its jugal element articulates directly with the squamosal, in which respect it accords with that of the Dicynodont Reptiles, and should be known as a squamoso-maxillary arcade. According to the view of Professor Huxley, the Sauropsidan quadrate has been taken up into the inner ear to form the malleus. More recently, however, other writers have taken a different view, and, according to Dr Baur, the representative of the quadrate is to be found in the zygomatic process of the squamosal, with which the jugal articulates; the quadratojugal being also represented at the junction of these two bones. Dr Gadow, however, disputes this view, and finds the representative of the quadrate in the tympanic ring, this determination according with the view here taken as to the homology of the zygomatic arcade, which appears to have no quadratojugal element.

Again, when, as in the Primates and many Ungulates, the orbit is bounded posteriorly by a bony postorbital bar, the ascending process of the jugal articulates directly with the frontal, without the intervention of the postorbital or postfrontal, which forms such a conspicuous feature in the Reptilian skull.

In all cases the premaxillæ, maxillæ, and palatines develop inferior palatal plates which meet in the median line below the nasal passage, and thus completely separate the latter from the cavity of the mouth. Except, however, in the Anteaters (*Myrmecophaga*), in one genus of Armadillo (*Tatusia*), in certain Cetaceans, and in one species of *Hyænodon*, this flooring of the nasal passage does not extend backwards to include the pterygoids, as it does in modern Crocodilians. The palatines are always placed behind the maxillæ.

Finally, the sclerotic of the eyeball never develops a ring of bony plates like that so frequently found in the Sauropsida.

A characteristic feature of the larger bones of Mammals, although one by no means peculiar to the class, consists in their ossifying from several distinct centres. In the case of the long bones the shaft is formed by one centre of ossification, while two distinct elements termed epiphyses form the extremities; in the adult the whole of these being welded together into a solid mass. The long bones are also tubular, and their vacuity is filled with the fatty marrow.

The vertebræ always have well-developed articular processes on their arches; the ends of the centra are generally flattened, but in the cervical region of certain Ungulata they may be opisthocœlous. Terminal epiphyses, so generally wanting in the Sauropsida, are nearly always present. The number of vertebræ varies greatly, owing to the great difference in the length of the tail in different species; but in the majority of Mammals the number of precaudal vertebræ does not vary very far from thirty, although in *Hyrax* and *Cholœpus* their number reaches forty. In spite of the great difference in the length of the neck in different Mammals, the number of cervical vertebræ in existing forms is, with three normal exceptions, seven. These exceptions are *Manatus australis* and *Cholœpus Hoffmanni*, in which the number is reduced to six, and *Bradypus tridactylus*, in which it is increased to nine. According, however, to Professor W. K. Parker there may occasionally be eight cervicals in the Pangolin (*Manis*). The first, or atlas, vertebra always has two articular cups for the occipital condyles; and, except in certain Cetacea, the second, or axis, has a well-defined odontoid process. Usually the cervical vertebræ are quite free; but they are anchylosed together in some of the Cetacea, and in the Armadillos. The dorsal vertebræ are usually well defined from the lumbar, although this is not invariably the case; and the number of dorso-lumbars in any one given group is usually very constant, and among the Ungulata affords assistance in classification. A distinct sacral region is present in all Mammals except the Cetacea, where the iliac bones are absent. The number of caudal vertebræ varies from three (certain Primates) to forty-six (*Manis*). Chevron-bones are present in the caudal region of many long-tailed forms. The sternum is always present, although varying greatly in form. It usually consists of a *presternum* (fig. 1128, *p*) and of a posterior *xiphisternum* (*x*), between which are a varying number of segments (*m*) constituting the *mesosternum*. The segments of the mesosternum (fig. 1128, A) may be anchylosed together; and in the *Balænidæ*, among the Cetacea, only the presternum is present. The connection of the ribs with the sternum is generally by cartilage; but in the Armadillos the costal cartilages ossify, and are then

known as *sternal ribs*. In the anterior dorsal region the capitular head of the ribs articulates with the vertebræ in a pit at the junction of two centra, while the tubercular head joins the transverse process of the second of these two vertebræ; but in the posterior dorsal region the two heads generally coalesce. Dr Baur regards the intervertebral articulation of the capitula in the anterior region as a direct survival of the intercentral attachment of the ribs of primitive forms allied to Theriodont Anomondontia, which has been totally lost among other Reptiles; and the mode of costal articulation is

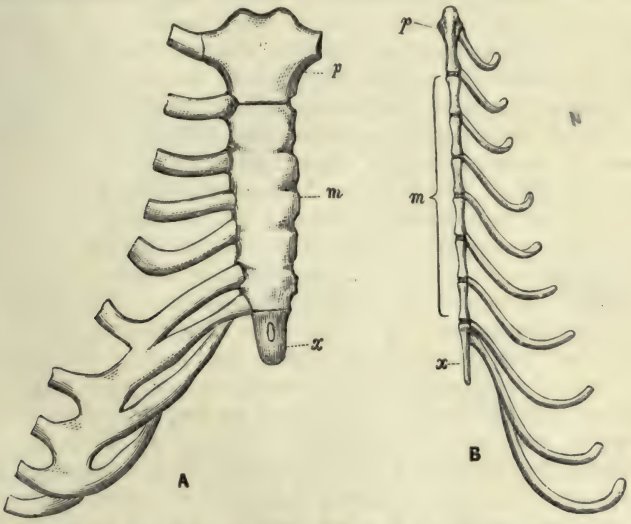


Fig. 1128.—A, Sternum and right costal cartilages of Man; B, Sternum and left costal cartilages of Dog. *p*, Presternum; *m*, Mesosternum; *x*, Xiphisternum.

undoubtedly very near to that of those Anomodonts which have lost the intercentra. Uncinate processes are never present on the ribs.

In all Mammals the pectoral limb is well developed. The pectoral girdle is, however, usually simpler than in lower forms; the coracoid persisting as a distinct bone only in the Monotremata, where, however, it anchyloses to the scapula. An interclavicle is present only in the last-named order; where it articulates with the clavicles after the Reptilian manner. In the Eutheria the clavicles only retain their complete development in those groups, such as the Insectivora, many Rodentia, the Chiroptera, and the Primates, which use the pectoral limb for flight, burrowing, or prehension. The humerus frequently has an entepicondylar foramen, like that of the Anomodont Reptiles. The radius and ulna retain their original

pre- and postaxial position in the Cetacea; but in most other Mammals they are crossed at their distal ends, so that their positions become reversed, and in the "prone" or normal position of the limb the radial, or preaxial border of the hand, becomes internal. In the Primates, however, these bones admit of motion upon one another; and when the hand is "supine" (that is, with its palm directed forwards or upwards), the bones of the fore-arm occupy their original primitive position. In the majority of those Mammals whose limbs are adapted solely for walking, the ulna is more or less reduced, and the radius, especially at its proximal end, is much enlarged, so that it articulates with the whole of the anterior surface of the humerus; and thus comes in front of the ulna, instead of at its side. The carpus essentially corresponds with that of the type represented in fig. 829 (p. 907); the radiale,[1] intermedium, and ulnare being termed the scaphoid, lunar, and cuneiform; the trapezium, trapezoid, and magnum representing the 1st, 2d, and 3d carpalia, and the unciform the 4th and 5th of that series. A centrale is present in the carpus of embryos of pentedactylate forms; but in the adult it usually fuses with the scaphoid, although it remains distinct in most of the Primates. In some groups others of these elements may also coalesce, and one or more may be absent. The pisiform, or presumed representative of the seventh digit, is generally well developed; while in pentadactylate types there may be an ossification representing the prepollex. The metacarpals and digits may be five in number (Proboscidea and Primates), or may be reduced to two, or even to one functional member. Among the Ungulata, when the metacarpus is reduced to a single functional element, as in the Horse, such element is frequently termed the *cannon-bone;* in anatomy, however, this term is more usually restricted to the metapodium of those Artiodactyla which consists of the coalesced third and fourth metapodials. Except in the Cetacea there are never more than three phalangeals to each digit, but by suppression or anchylosis this number is occasionally reduced; and the first digit (pollex) has but two phalangeals. The pelvic girdle is also fully developed in all Mammals except the Cetacea and Sirenia; and in the adult the three elements coalesce to form an *innominate* bone. The pubis and ischium of the same side always unite to enclose the obturator foramen; and the two pubes meet in a ventral symphysis, which is, however, not completely united in certain Insectivora. In a large number of instances the ischia meet in a ventral symphysis,

[1] Since the preceding chapters were in type, Dr Baur has expressed his opinion that the bone termed radiale in fig. 829 is really a second centrale; and that the radiale is represented by a minute bone generally known as the radial sesamoid. The Mammalian scaphoid is accordingly also regarded as a second centrale. In the same communication, Dr Baur expresses his disbelief in the existence of remnants of a prepollex and of a seventh digit in Mammals and other Vertebrates.

which is greatly elongated in some Ungulates (fig. 1128 *bis*), but in the Primates and some other forms there is no such union. In the Monotremata and Marsupialia epipubic, or *marsupial*, bones are attached to the anterior border of the pubic symphysis (fig. 1139). The femur may have a third trochanter (fig. 1226) for the attachment of one of the gluteal muscles. The tibia and fibula are never crossed at their distal extremity, but lie in their primitive parallel position; the tibia, or preaxial bone, being internal in the usual walking position, and the fibula external. The latter bone may be more or less rudimentary, and completely anchylosed at one or both

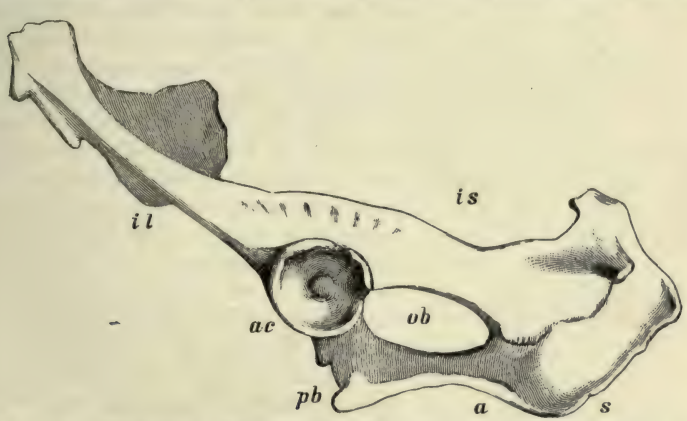


Fig. 1128 *bis*.—The left side of the pelvis of the Eland (*Oreas canna*). One-sixth natural size. *il*, Ilium; *is*, Ischium; *s*, Symphysis of do.; *a*, Epiphysis on symphysis of ischium and pubis; *pb*, Pubis; *ob*, Obturator foramen.

extremities to the tibia. The patella is present in all except some Metatheria. If the pes (fig. 1129) be compared with the typical tarsus mentioned on p. 907, it will be found that the fibulare is represented by the calcaneum, which may also contain an element corresponding to the pisiform of the manus; the astragalus has been usually regarded as the coalesced tibiale and intermedium, but is thought by Dr Baur to correspond solely to the latter; the ento-, meso-, and ectocuneiform represent the 1st, 2d, and 3d tarsalia; while the 4th and 5th tarsalia have coalesced to form the cuboids. The centrale persists as the navicular, which may unite with the cuboid.[1] Other modifications occur analogous to those in the carpus; but in no instance, as already observed, is the joint between the leg and the pes formed on the line between the proximal and distal rows of the tarsus. The metatarsals and phalan-

[1] Dr Bardeleben has pointed out to the writer that in *Cryptoprocta* there may be a second centrale, which usually coalesces with the ectocuneiform.

geals repeat the characters of the homologous bones of the manus, although they deviate in a lesser degree from a common type. In the Cetacea and Sirenia the pes is entirely absent; although the proximal portions of the pelvic limb may be detected in an aborted form in many genera.

We may now take a brief glance at the general distribution in time of the Mammalia, in the course of which we shall have to forestall some of the information given in the sequel.

If the theory of evolution be the true explanation of the order of nature we should expect to find that the earliest representatives of the class would be small forms, more or less closely related to one another, not numerous in generic types, and allied to those orders which now comprise the most generalised representatives of the class. Our knowledge of these earlier types is indeed exceedingly imperfect, but so far as it goes it appears to accord fairly well with the foregoing conditions; all the earlier forms being of small size, and apparently more or less closely allied to the existing Marsupials, and probably also to the Monotremes and perhaps the Insectivores. The earliest evidence of the occurrence of Mammals yet known is in the upper portion of the Triassic system, which forms the base of the great Mesozoic period. Of the two known genera from these deposits the larger type, termed *Dromatherium*, exhibits some curious approximations in the structure of its teeth to Reptiles and Amphibians, and it is possible that we may have in this form an ancestral type of the Prototheria. In the Lower Jurassic, immediately above the Lias, remains of small Mammals become more common, and in the Upper Jurassic they are locally abundant, although they comprise comparatively few generic types. These Jurassic Mammals are readily divisible into two groups, distinguished by the characters of their teeth. Of the first group an example of the lower jaw is shown in fig. 1141, p. 1274, where it will be seen that the teeth are very numerous, the hinder ones having several sharp cusps on the crowns. Although there has been much discussion as to the affinities of these small Mammals, it is probable that they are really Marsupials of the suborder Polyprotodontia, with a relationship to the Australian Anteater (*Myrmecobius*), which,

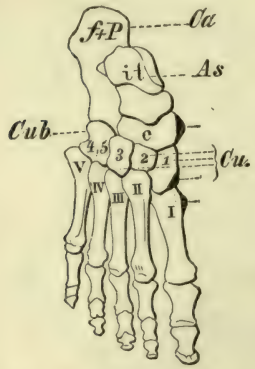


Fig. 1129. — Dorsal aspect of the right pes of Man. Reduced. *Ca*, Calcaneum (fibulare + ? pisiform); *As*, Astragalus (intermedium); *c*, Navicular (centrale); *Cu*, 1-3, Ento-, meso-, and ectocuneiform (1st, 2d, 3d tarsalia); *Cub*, Cuboid (4th, 5th tarsalia); i-v, Metatarsals. (After Wiedersheim.)

as we shall see in the sequel, is the only existing heterodont Mammal with more than four true molars. In the second group the dentition is of a very different type; the lower jaw having a single pair of curved and chisel-like incisors, separated by an interval from the cheek-teeth, which are characterised by the presence of one or more longitudinal grooves. The serial position of this group, which has been named Multituberculata, is still open to doubt, but not improbably it may indicate an extinct order of Prototheria.

Throughout the greater part of the Cretaceous period our knowledge of Mammalian life is a blank, doubtless owing to the circumstance that the greater portion of the Cretaceous beds, such as the Chalk, is of purely marine origin; but evidence has recently been obtained of the existence of a Mammalian fauna in the topmost Cretaceous of North America allied to that of the Jurassic.

With the dawn of the Tertiary period, which may be regarded as the first commencement of the present order of nature, we meet, however, with an abundant Mammalian fauna, containing representatives of nearly all the existing orders, but also including several subordinal types now totally passed away, some of which are of extreme interest to the zoologist as connecting together more or less completely groups which are now widely separated. In the Eocene we are indebted to the palæontologists of the New World for most of our knowledge of these primitive connecting links; but we can only afford space to notice very briefly some of the more interesting groups.

Of Carnivorous types there is a group of Eocene genera known as the Creodonta, remarkable, among other features, for their generalised dentition, which has resemblances to that of the Polyprotodont Marsupialia and Insectivora, and also to that of the modern Carnivora, of which these forms were probably the ancestors. We thus have indications how the Carnivora of the present day may have been gradually evolved from a Marsupial type by means of forms more or less nearly related to the Insectivora of the present epoch. In another direction the Eocene has afforded evidence of a transition from the Insectivorous type towards that of the Lemuroid Primates, and we may thus readily conceive how the higher members of the latter order may likewise trace back their origin to the same primitive stock.

At the present day no orders of Mammals appear more sharply defined from one another than the Carnivores and the Ungulates. In the Eocene, however, we meet with a group of primitive Ungulates, known as the Condylarthra, presenting such remarkable resemblances to the primitive Carnivores, that we are led to the conclusion that the Ungulates are probably another branch derived

from this same prolific stock. From this Condylarthrous suborder we have abundant evidence that the two existing suborders of the Artiodactyla and Perissodactyla, now so sharply distinguished, have both taken their origin; and perhaps the Hyracoidea may also trace their derivation from this group. Another extinct Eocene suborder of Ungulates, comprising the Coryphodons of Europe and America, and the huge and uncouth Dinocerata of the United States, tends to show a connection between the Perissodactyla and Proboscidea, which till recently were referred to distinct orders.

All living Ungulates, as we shall subsequently mention, are distinguished by the total absence of clavicles, but in the remarkable *Typotherium*, of the Pleistocene of South America, these bones were retained. In its dentition, moreover, that genus shows features now peculiar to the Rodents; and by its help, together with the evidence afforded by an Eocene group known as the Tillodonts, we can dimly see how the Rodents may have been connected with the ancestors of both the Ungulates and the Carnivores.

Having seen from these brief notices how intimate appears to have been the relationship between the chief terrestrial orders of Mammals in the Lower Eocene, we may glance at the evidence afforded by the Mammals of the Eocene as to the connection between some of the families of these orders. Among the Carnivora, no two families are better distinguished than the Dogs, or *Canidæ*, with their triangular upper molars and digitigrade feet, and the Bears, or *Ursidæ*, in which the upper molars are rhomboidal and the feet are plantigrade. In the Eocene, however, we have *Amphicyon*, with the teeth of a Dog and the limbs of a Bear; and in the later Tertiary the Bear-like *Hyænarctus*, of which the dentition retains many Dog-like features. So perfect, indeed, is the transition between Dogs and Bears, that it seems convenient to include both groups in a single family. Again, in another direction, the Dogs of the Eocene seem to pass imperceptibly into the Civets (*Viverridæ*) through *Cynodictis;* while it is almost impossible to distinguish the Civets from the Hyænas on the one hand, and the Cats (*Felidæ*) on the other. Still more remarkable is the apparent connection in the Eocene of the Civets with the Weasels (*Mustelidæ*), since these two families are widely sundered at the present day.

Turning to the Ungulates, at the present day the Artiodactylate suborder can be readily divided into four sections—viz., the Pigs, or Suina; the Camels, or Tylopoda; the Chevrotains, or Tragulina; and the Cattle and Deer, or Pecora. When, however, we go back to the early Tertiary, we find a complete transition from the Suina to the Pecora; while it is almost impossible to distinguish Deer from Chevrotains; and the early Camels exhibit signs of close

connection with the other families. Similarly, at the same period the Pigs of the Old World appear to be inseparable from the Peccaries of the New; while the Giraffes were probably as closely connected with the Antelopes on the one hand, and the Deer on the other. Again, in the Perissodactylate suborder Tapir-like forms appear to have passed into Rhinoceroses on the one hand, and into the Horses on the other.

Many other equally striking instances could be cited of the mutual connection of the Eocene Mammals with one another; but enough has been stated to show that the present sharply defined distinction of the orders and families into which we find it convenient to divide the class is, so to speak, but a feature of to-day.

In the Lower Eocene all the genera of Mammals appear to be extinct; but in the Upper division of the same period, which is frequently termed the Lower Oligocene, we meet with a few existing genera, such as *Didelphys*, *Rhinoceros*, *Viverra*, *Mustela* (Weasel), and perhaps *Canis*. In the succeeding period, or Miocene, existing genera become more common; thus in the Lower and Middle divisions of that period we meet with Otters (*Lutra*), *Rhinoceros*, Tapirs (*Tapirus*), and Gibbons (*Hylobates*). The middle division of the Miocene is, indeed, noteworthy for the appearance of Anthropoid Apes and the Proboscidea, or Elephants and Mastodons. Deer of extinct genera are abundant; but these were either devoid of antlers, or, if these appendages were present, they were small and simple. The teeth of the Ruminant Ungulates (Deer and Cattle) were, moreover, low-crowned or brachydont (fig. 1213), and the Rhinoceroses had in most cases not yet developed horns.

With the commencement of the Pliocene period the Mammalian fauna assumes a much more modern appearance. Thus we have Porcupines (*Hystrix*), Hyænas, large Tiger-like Cats (*Felis*), numerous Antelopes, Giraffes, Deer (*Cervus*), and Horse-like animals (*Hipparion*); while in India true Elephants (*Elephas*) had made their appearance. There was still, however, a large number of extinct genera. By this time many of the Deer had acquired complicated antlers; many of the Ruminants had tall-crowned or hypsodont teeth; the Rhinoceroses had horns; and the Pigs had developed large tusks in the males. In India during some portion of the Pliocene, not only Elephants, but true Horses (*Equus*), Hippopotami, Wolves, Bears (*Ursus*), and Oxen (*Bos*) had already made their appearance; but in Europe these genera are unknown before the top of the Pliocene, when we first meet with remains of a few existing species, such as the African Hippopotamus and the Striped Hyæna.

In the succeeding Pleistocene period, which may in reality be

regarded merely as the commencement of the epoch in which we are now living, the greater number of the Mammals of Europe belong to existing genera, and a considerable proportion of these to living species. The fauna of Europe in the early part of this period included, however, a large number of Mammals belonging to genera or species now confined to the warmer regions of the globe, such as Rhinoceroses, Hippopotami, Elephants, Lions, Hyænas, &c.; and it was not till after the great cold of the glacial period that these generic types were finally swept away from the European area. In many other parts of the World the Pleistocene period was equally prolific in large forms of Mammalian life, more or less closely allied to those now inhabiting the same areas, of which we have remarkable instances in the extinct Edentates of South America and the Marsupials of Australia, many of which vastly exceeded in size their living relatives. Science has, indeed, yet to account satisfactorily for the disappearance of this exuberant life, and the consequently impoverished fauna among which we now dwell.

In regard to the Mammals of the Eocene, we have already remarked that they are frequently of a more generalised type than those now existing, and in many groups a well-marked progressive specialisation can be traced as we approach the existing epoch. Thus many of the Eocene Mammals possess the full Eutherian complement of forty-four teeth, which in the Ungulates were more uniform in size, less conspicuously differentiated into groups, and more approximated to one another than in recent forms. In the older Ungulates, moreover, the crowns of the cheek-teeth were relatively short; and we can trace a gradual increase in the height of the crowns as we advance in time, this increase affording a greater capacity to withstand wear, and thus indicating a greater length of life in the individual. In other instances we may observe a gradual reduction in the lateral digits of the typical pentedactylate limb, accompanied by a progressive elongation and strengthening of one or more of the remaining digits. Again, it has been shown that there has been a gradual increase in the relative size and the complexity of the brain as we approach the present day. Thus the Eocene Mammals, as a rule, had very small brains, in which the hemispheres left the cerebellum nearly uncovered, and were themselves nearly smooth, or but slightly convoluted; while in the higher forms the hemispheres spread backwards over the cerebellum, and are often marked by most complex convolutions. In some Eocene Ungulates the brain was so small that it could pass through the neural canal of the lumbar vertebræ.

Finally, it should be observed that we may trace a gradual evolution of local faunas. In the Eocene of any given region we find the Mammals differing widely in generic types from those now in-

habiting that area, yet as we ascend in the geological scale we trace a gradual approximation to the existing fauna; and in the Pleistocene we find the characteristic features of such fauna distinctly marked out, although many of the generic types, especially those including forms of large corporeal bulk, may be different. Examples of these features are afforded by the Marsupials of the Pleistocene of Australia, and the numerous Edentates of the same period in South America; although it is practically certain that in the former case the fauna has always been Marsupial, and therefore more or less closely related to the present one. That many of the existing Mammalian faunas now characteristic of particular regions were not thus circumscribed till a late period is, however, shown by the occurrence of Baboons, Hippopotami, Giraffes, and African types of Antelopes in the Pliocene and Pleistocene of India and parts of Europe; and equally by the Mammals of the Pleistocene of India being in many cases specifically identical with those of Africa, while the number of common species is now very few indeed. Again, many forms like the Rhinoceroses and Horses, which are now exclusively Old World types, formerly wandered over the plains of America, and thus point to a more uniform distribution of types than now exists. There are, however, indications of certain groups of Mammals having always been restricted to one hemisphere. Thus we have no evidence of the existence of Apes, Hyænas, or Civets at any epoch in the New World; and neither are there any traces of the Dinocerata or *Titanotheriidæ* in the Old World.

It was considered probable some years ago that the Mammalia were directly descended from some primitive Amphibian types, and that they stood altogether apart from the Reptiles. The striking resemblance of the pectoral girdle of the oviparous Monotremes to that of many Reptiles, and more especially the Anomodonts, together with the remarkable approximation to a low Mammalian type presented by the skeleton of the latter, renders it, however, more probable that Mammals are a divergent branch of the same Amphibian stock which gave origin to the last-mentioned group, if indeed they be not the direct descendants of the earlier forms of that group. Dr Baur, who considers that Mammals were developed from true Reptiles allied to the primitive Rhynchocephalia and Sauropterygia, has proposed that these early hypothetical forms should be termed Sauromammalia. Professor Mivart has, indeed, suggested that Mammals may have had a dual origin; and that while the Monotremes may have been derived at a comparatively late date from the Anomodonts or kindred types, the Marsupials may have originated at an earlier epoch from a totally distinct and perhaps Amphibian stock. Many objections have, however, been raised against this view; and Mr Poulton expresses his opinion that

"whether the Monotremes are the descendants of the ancestral Mammalia or not, it is quite certain that the higher Mammals must at one time have passed through a condition such as now exists in the Monotremes, in nearly all parts of their organisation; and many powerful arguments can be brought against the assumption that the same stage has been reached independently, and at widely separated periods, in the course of evolution." [1]

In the following chapters are given the leading palæontological characters of each order of the class, with the range in time of the different groups, and the names of the more important genera. The number of genera is, however, so great that only a very brief and general sketch of their characters and affinities can be given; special attention being drawn, where it may seem necessary, to those extinct types which are of more than ordinary interest from an evolutionary point of view.

[1] The opinion has been recently expressed by some Continental writers that the Cetacea are the most archaic type of Mammals, and that they have been directly derived from the Ichthyopterygian Reptiles. There is, however, so much evidence against this view that it may be considered as practically disproved.

CHAPTER LIX.

CLASS MAMMALIA—continued.

Orders Monotremata and Marsupialia.

Subclass I. Prototheria.—This subclass, now represented by only two genera, may be characterised as follows. The brain has a large anterior commissure, and a very small corpus callosum;[1] while the auditory ossicles are simple, and the stapes is rod-like (columelliform). The coracoid is a distinct, although small, bone, anchylosing in the adult to the scapula, and articulating with the sternum; while there is a separate precoracoid (epicoracoid), which does not articulate with the scapula, and also a large T-shaped interclavicle; the form and relations of these bones being very like those of the corresponding parts of the skeleton in the Anomodont Reptiles. The pelvis has epipubic bones, and the ilia are inclined to the sacral axis after the Batrachian fashion; thus resembling those of the Pariasaurian Anomodonts. The urinogenital and excretory organs open into a common outlet, or *cloaca;* and the former are very similar to those of the Sauropsida; the mammary glands are unprovided with nipples, and the reproduction is oviparous; the eggs being meroblastic like those of Birds.

It may here be observed that the small bone in the pectoral girdle of the Monotremes placed in advance of the coracoid, which is usually termed the epicoracoid, appears to correspond with the precoracoid of the Anomodont Reptiles[2] (fig. 978 *bis*, p. 1054), although it does not extend upwards to articulate with the acromial process of the scapula, as the Anomodont precoracoid articulates with the process of the scapula identified by Sir R. Owen with the acromion.[3] Further, the scapula of the Monotremes differs from that of all other Mammals, and resembles

[1] The structure connecting the two hemispheres of the brain.

[2] This appears to be the view taken by Professor Cope.

[3] This is the original view. In describing the scapula of *Platypodosaurus*, Sir R. Owen confused the process situated above *a* in fig. 978 *bis* with that marked *a*, and termed the former the acromion.

that of Reptiles in that the acromion is situated on the anterior or preaxial border, which in the higher Mammals has become twisted round to the dorsal surface to form the spine of the scapula. The scapula of some of the Anomodont Reptiles appears to indicate how this torsion of the preaxial axial to form a ridge on the dorsal surface has taken place.

At the close of the preceding chapter reference has been made to the relationship of the Prototheria, or rather of its existing representatives the Monotremata, to Reptiles and Amphibia. The structure of the pectoral and pelvic girdles presents, indeed, so many striking resemblances to the same parts of the skeleton in the Labyrinthodont Amphibia and Anomodont Reptiles, as to indicate, as already mentioned, a distinct genetic connection between the three groups; the characters of the humerus apparently indicating

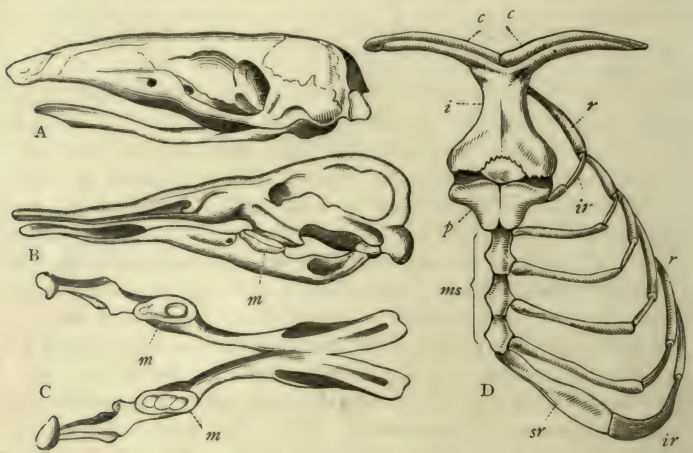


Fig. 1130.—A, Lateral view of skull of *Echidna*; B, Do. of *Ornithorhynchus*: C, Oral view of mandible of do.; D, Sternal region of do. *c*, Clavicle; *i*, Interclavicle; *p*, Presternum; *ms*, Mesosternum; *r*, Ribs; *sr*, Sternal ribs; *ir*, Intermediate ribs; *m*, Cornules. Reduced. (D after Flower; the others after Giebel.)

that the nearest relationship is with the Anomodonts. The deciduous teeth of *Ornithorhynchus* indicate, moreover, without any doubt that the ancestors of the Monotremes were provided with persistent teeth, which were probably monophyodont. Moreover, a distant resemblance between these deciduous teeth and the cheek-teeth of the extinct group, mentioned below under the name of Multituberculata, suggests that these forms may themselves be Prototheria. If this should prove to be the case, it would then be apparent that that branch of the subclass could not have been the ancestral stock of the Marsupials; and we shall accordingly have to look for another group or order of Prototheria, with a dentition akin to that of the Polyprotodont Marsupials. It is,

indeed, quite within the bounds of probability that the family *Dromatheriidæ* mentioned under the head of the latter group may prove to be Prototherians. And in any case it is quite evident that the two existing genera of Monotremes can in no way be looked upon as actual ancestral types.

ORDER I. MONOTREMATA.—As already mentioned, both the existing genera of Prototherians are included in this order, which may be provisionally characterised by the production of the cranium into a more or less elongated rostrum supporting a horny beak; by the absence of teeth in the fully adult animal; the smoothness of the brain-case; and the absence of an auditory bulla. The humerus is greatly expanded, and has an entepicondylar foramen; its whole contour approximating to the corresponding bone of the Anomodont Reptiles (fig. 982).

FAMILY ORNITHORHYNCHIDÆ.—In this family the cerebral hemispheres are smooth; the extremity of the muzzle is produced into a

Fig. 1131.—*Ornithorhynchus paradoxus*, Australia. Reduced.

broad beak-like expansion (fig. 1131); teeth are present in the young, and are succeeded by horny plates or cornules (fig. 1130, B, C); and the skin is covered with hair. The feet are webbed. This

family is represented solely by the genus *Ornithorhynchus* (fig. 1131), of which a single species inhabits the Australian rivers, in the banks of which its burrows are constructed. According to the observations of Mr O. Thomas, it appears that there are usually two teeth on either side of the upper and three in the lower jaw, which persist till the animal is somewhat more than one-third grown. These teeth have at first small but distinct roots, and present a distant resemblance to the true molars of some of the Multituberculata, like *Microlestes;* one of their longitudinal walls, or ridges, carrying a number of minute cusps. It appears that the cornules grow up beneath and around these teeth, which are gradually worn away, and finally shed like the milk-molars of other Mammals; the hollows in the cornules being the remnants of the original alveoli.

Family Echidnidæ.—The second family is characterised by the convoluted cerebral hemispheres; the production of the muzzle into a long tube-like beak (fig. 1130, A); the slenderness of the mandible; the total absence of teeth; and the presence of stout spines mingled with the fur. Further, the feet are very strong, and adapted for digging, and the centre of the acetabulum is imperfectly ossified. There are two living species found in Australia and New Guinea, both of which, at least for palæontological purposes, may be included in the genus *Echidna*, although the large *E. Bruijnii*, of New Guinea, is frequently separated under the name of *Proechidna*. Remains of a large species considerably exceeding the latter in size have been obtained from the Pleistocene of New South Wales.

Group Multituberculata.—In this place it will be convenient to notice a group of very imperfectly known Mesozoic and early Tertiary Mammals which were formerly regarded as Diprotodont Marsupials allied to *Thylacoleo*, but which differ in several respects from that group, and may perhaps eventually prove to be members of the subclass Prototheria. Although these peculiar forms resemble the Diprotodonts in having a single pair of lower incisors like those of Rodents, while many of them also approximate to certain members of the same group in having a secant and grooved fourth premolar; yet they differ in that it is the second in place of the first upper incisor which becomes enlarged and opposed to the incisor of the lower jaw; while when the fourth lower premolar is secant the summit of its crown is extremely convex instead of more or less concave. The true molars, as already mentioned, appear to approximate in general structure to the deciduous cheek-teeth of *Ornithorhynchus*, and are quite unlike those of any recent Marsupials. Till, however, the structure of the pectoral girdle be known the serial position of these forms cannot be definitely determined. And it may be observed, that the humerus of the limb which may be referable to *Tritylodon* is unlike that of the Mono-

tremata, so that if these forms be Prototheria they probably indicate a distinct specialised order of that subclass.

In addition to the features mentioned above, this group is characterised by the true molars (fig. 1136) carrying longitudinal rows of tubercles, separated by one or more grooves, and also by the absence of a pit or perforation in the masseteric form of the mandible.

Family Plagiaulacidæ.—In the *Plagiaulacidæ* the premolars, which vary in number from one to four in the mandible (figs. 1132–

Fig. 1132.—A, Outer view of the right ramus of the mandible of *Plagiaulax minor;* four times natural size. B, Fourth lower premolar of *P. Becklesi;* five and a half times natural size. From the Purbeck of Dorsetshire. (After Owen.)

1138), are always of a secant nature, and are usually marked by a series of oblique lateral grooves (fig. 1132); while the true molars are small and reduced to two in number. In the type genus *Plagiaulax* of the Purbeck (Upper Jurassic) of Dorsetshire, there may be either four (fig. 1132), or three lower premolars; Professor Cope regarding the latter variation as indicating a distinct genus, for which he has proposed the name *Plioprion*. The upper teeth are unknown. *Ctenacodon* (fig. 1133), from the Upper Jurassic of North America, is a closely allied but perhaps less specialised type, with four lower premolars, which are much worn in the figured specimen. In the upper jaw the anterior premolars are like those of *Bolodon*. The figure shows the relatively low position of the condyle of the mandible in this family;—a feature shared with the Pleistocene *Thylacoleo*, among the Marsupials. From the Lowest Eocene, both of France and North America, we have the more specialised genus *Neoplagiaulax* (fig. 1134), in which only the fourth premolar remains in the mandible. The Puerco Eocene of North America has also yielded *Ptilodus* (fig. 1135), characterised by the

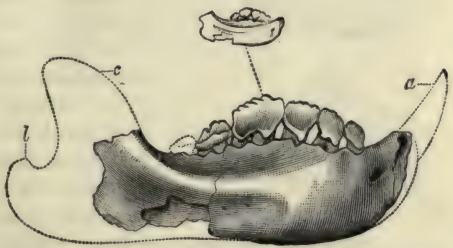


Fig. 1133.—Outer aspect of the right ramus of the mandible of *Ctenacodon serratus;* from the Upper Jurassic of North America. Upper figure, natural size; lower, four times natural size. *a*, Incisor; *b*, Condyle; *c*, Coronoid process. (After Marsh.)

presence of a minute third lower premolar. *Liotomus* of the French Eocene differs from all the others by its smooth fourth premolar. *Meniscöessus*, from the uppermost or Laramie Cretaceous of the United

Fig. 1134.—Inner view of the left ramus of the mandible of *Neoplagiaulax eocænus*; from the Lower Eocene of Rheims. The line indicates the true size. (After Lemoine.)

States, is a somewhat larger form which may probably be included in this family. It was first made known by an upper true molar, but secant premolars from the same deposits subsequently described under the name of *Halodon*, together with other teeth figured under the names of *Tripriodon*, *Diprodion*, and *Selenacodon*, are probably all referable to *Meniscöessus*. Another form from the Laramie Cretaceous which may be provisionally known as *Cimoliomys*, appears to be closely allied to the Eocene *Ptilodus*, but may have affinity with *Plagiaulax*; the teeth described as *Cimolodon* and *Nanomys*, as well as one of those referred to *Halodon* appear inseparable from this form. Other generic names have been applied to teeth of a more or less closely allied type from the same deposits.

Fig. 1135.—The left ramus of the mandible of *Ptilodus mediævus*; from the outer (*a*), inner (*b*), and oral (*c*) aspects: from the Puerco Eocene of New Mexico. (After Cope.)

Certain bones from the Laramie described as *Camptomus* probably belong to this group, and are noteworthy as showing a distinct coracoid and interclavicle; thus, if rightly referred and determined, clearly indicating the Prototherian affinities of the Multituberculata.

From the Tertiaries of Patagonia Dr Ameghino has described certain remains under the generic names of *Abderites*, *Acdestis*, and *Palæotheutes*, which are referred to this family, and are apparently nearly related to the European genera. The genus *Microbiotherium*

has also been described from the same deposits, and is regarded as indicating a distinct family.

FAMILY POLYMASTODONTIDÆ.—The type genus *Polymastodon* occurs in the Lowest Eocene of North America, and has one premolar and two true molars. The premolar is tubercular, and the upper true molars have three longitudinal ridges, and are elongated antero-posteriorly.

FAMILY TRITYLODONTIDÆ.—The genus *Tritylodon* was first described from a nearly entire cranium found in the Karoo system of South Africa, in a horizon which is probably of Lower Mesozoic age; but a tooth (fig. 1136) previously obtained from the Upper Trias of Germany, and described under the preoccupied name of *Triglyphus*, proves to belong to the same genus. The upper dental formula is *I.* 2, *C.* 0, *Pm.* 2, *M.* 4. The innermost upper incisor is large and scalpriform, while the outer one is very minute. The upper true molars (fig. 1136) carry three longitudinal ridges, and have the longer diameter of the crown directed transversely. The anterior portion of the cranium is remarkable for its great width and bluntness. The African species indicates an animal about the size of a Rabbit. From the same deposits at the Cape has been obtained a slab showing the impression of a pectoral limb apparently referable to a small Mammal, which has been described under the name of *Theriodesmus*. If, as is probably the case, this specimen be really Mammalian, there is, however, no reason why it should not belong to *Tritylodon*. According to Professor Bardeleben this limb has two centralia in the carpus (as in some Insectivora), and a distinct prehallux; the alleged fusion of the scaphoid with the lunar being incorrect. To the present family may likewise be referred the very imperfectly known *Stereognathus*, of the Lower Jurassic of Stonesfield; the upper cheek-teeth of which closely resemble those of *Tritylodon*. Finally, *Chirox*, from the Upper Jurassic of North America, shows certain characters connecting the present with the next family, in which it is provisionally placed by Professor Osborn.

Fig. 1136.—An upper true molar of *Tritylodon Fraasi*; from the Upper Trias of Strasbourg. The two central figures are of the natural size; the others enlarged three times. *o*, Crown surface; *u*, Basal surface; *v*, *h*, The two lateral surfaces; *i*, *a*, Anterior and posterior surfaces. The position of *o* is at right angles to that of the molars in the next figure.

FAMILY BOLODONTIDÆ.—Nearly allied to the preceding family, but with the upper true molars antero-posteriorly instead of transversely elongated, and with only two longitudinal ridges, is the

genus *Bolodon*, of the Dorsetshire Purbeck. In this genus (fig. 1137) there were apparently three upper premolars and four true molars; with probably three incisors, of which the first is very minute. Although of much smaller size, the cranium of the type species presents a striking resemblance to that of the African *Trityl-*

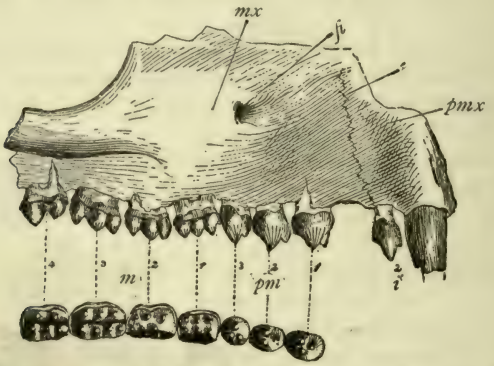


Fig. 1137.—The right maxilla of *Bolodon crassidens;* from the Dorsetshire Purbeck. *mx*, Maxilla; *pmx*, Premaxilla; *fi*, Foramen; *m*, True molars; *pm*, Premolars; *i*, Incisors. Greatly enlarged. (After Osborn.)

odon. *Allodon*, from the Upper Jurassic of North America, is a very closely allied, if not identical form, in which there were certainly three upper incisors, of which the second (fig. 1137) is enlarged, and apparently corresponds to the large inner incisor of *Tritylodon*. The genus *Microlestes*, from the Upper Trias of Würtemberg and England, is only known by detached molars (fig. 1138) closely resembling the true molars of *Plagiaulax*. This genus is referred by Professor Osborn to the *Plagiaulacidæ;* but till it is proved to have trenchant premolars it seems preferable to place it provisionally in the present family. Figure *a* in the accompanying woodcut gives a side view of the type tooth, which has two rows of tubercles separated by a longitudinal groove; the imperfect crown of another tooth shown in *b*, and provisionally referred to the same genus, is remarkable for the resemblance presented by its two remaining tubercles to those of the teeth of *Ornithorhynchus*. The name *Hypsiprymnopsis* has been applied to a tooth of *Microlestes*, from the English Rhætic.

a *b*

Fig. 1138.—*a*, Lateral view of a tooth of *Microlestes antiquus; b*, Part of the crown of a tooth on a still more enlarged scale; from the Upper Trias of Würtemberg. (After Lyell and Falconer.)

Subclass II. Metatheria.—The members of this subclass agree with the Prototheria in the structure of the brain and the presence

of epipubic bones[1] (fig. 1139, *m*), but differ in the more specialised characters of the auditory ossicles; in the reduction of the coracoid to a mere process of the scapula, and its non-articulation with the sternum; in the absence of an interclavicle; and in the presence of nipples to the mammary glands. In the latter characters they agree with the Eutheria, from which they are distinguished by the presence of an imperfect cloaca, and by the characters of the urinogenital organs, which are in some respects intermediate between those of the Eutheria and Prototheria. The young, although produced viviparously, are born in an exceedingly imperfect condition, and are never nourished *in utero* by an allantoic placenta; but at an early period are transferred to the nipples of the mother, to which they adhere for a long time. The nipples themselves are nearly always concealed in a fold of skin forming the so-called *marsupium*.

Fig. 1139.—Ventral view of the symphysis and left half of the pelvis of a Kangaroo. *m*, Epipubic bones. Reduced.

Teeth are invariably present, and are divisible into the usual four groups. With the exception of the *Phascolomyidæ*, the number of incisors in the upper jaw of all existing forms exceeds that in the mandible.[2] The true molars are very generally four in number on either side of each jaw; and in all existing forms the number of premolars does not exceed three, although four (which may be taken as the typical number) are found in several Mesozoic genera. The most remarkable feature about the dentition is, however, that it is only the last premolar (the fourth of the typical series) among the whole number of teeth that ever has a milk predecessor; such predecessor generally resembling the true molars in structure. Some genera, like *Phascolomys*, show, however, no signs of even this single replacement; and it is pretty clear that we have here the first commencement of a replacing series of teeth, which in the early Eutheria must have gradually extended anteriorly, until it normally embraced all the teeth in advance of *Pm.* 4, with the very general exception of *Pm.* 1, although in certain Perissodactyla even that tooth had a milk predecessor.

Another very characteristic, although not universal, feature in this subclass is the inflection of the angle of the mandible (fig. 1152);

[1] Unossified in *Thylacinus*.

[2] The same feature occurs among the Anomodont Reptiles in the *Galesauridæ*.

and in many genera the palatal region of the cranium contains unossified vacuities of considerable size.

ORDER II. MARSUPIALIA.—The whole of the known Metatheria are included in the single order Marsupialia, and it is not at present necessary to give ordinal characters as distinct from those of the subclass. At the present day this order is restricted to America and the Australian region; the greater number of forms occurring in the latter area, while only the *Didelphyidæ* are found in the former. In earlier epochs, however, this order was much more widely distributed, and it apparently contains some of the earliest known representatives of the entire class.

Marsupials form in some respects the intermediate stage between the Prototheria and Eutheria, and it is probable that there will be eventually found a complete transition from the Polyprotodont suborder of this group to unknown Prototherian Mammals with the same general type of dentition—possibly more or less closely allied to the undermentioned Triassic family *Dromatheriidæ*.

SUBORDER 1. POLYPROTODONTIA. — In existing Polyprotodont Marsupials, which occur both in America and the Australian region, there are never fewer than three lower and four upper incisors, and there may be five upper and four lower teeth of this series. These teeth are small and subequal, and are followed by a larger canine (fig. 1148). Normally there are three premolars, corresponding to the first, third, and fourth of the typical series, but the fourth may be absent, *Dasyurus* and *Sarcophilus* (fig. 1148). The number of true molars is generally four, but in *Myrmecobius* these teeth are increased to $\frac{5}{6}$; and their crowns are nearly always characterised by carrying a number of small, sharply pointed cusps. In no species is there a fourth premolar of the elongated secant form characteristic of many Diprotodonts. Several of the Mesozoic forms included in this group agree very closely with the recent ones, but many of them have four premolars, and in some there are as many as seven true molars.

FAMILY DROMATHERIIDÆ.—This family, typically represented by the genus *Dromatherium* (fig. 1140), of the reputed Trias of North America, is provisionally placed here, since it may be related to some of the members of the next family, although Professor Osborn makes it the type of a distinct order — the Protodonta — and even suggests that it may be Reptilian. If not Marsupials, these early Mammals may prove to be representatives of a group of Prototheria from which the Polyprotodont Marsupials have origin-

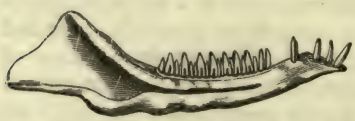


Fig. 1140.—Inner view of the left ramus of the mandible of *Dromatherium sylvestre*; from the Trias of North Carolina. (After Emmons.)

ated. The cheek-teeth differ from those of all other Marsupials in having the fangs imperfectly divided, and thus approximate to those of certain Anomodont Reptiles. There are seven true molars, the incisors are spaced, there is long diastema behind the canine, and the three premolars are of a very simple structure. The crowns of the true molars consist of one main cusp, with small accessory cusps; and it would appear that the teeth of the upper and lower jaws mutually interlocked. This type of tooth is regarded by Professor Osborn as the most archaic yet known. *Microconodon*, which occurs in the same deposits as *Dromatherium*, is an allied but smaller form.

Family Amphitheriidæ.—This Mesozoic family is provisionally taken to include a number of small and imperfectly known forms, some of which are regarded by almost all writers as undoubtedly Marsupials, although others have been referred by Professor Osborn, with some hesitation, to the Insectivora, under the name of Insectivora Primitiva; those which are retained by that writer in the present order being termed Prodidelphia. Although it is quite probable that with fuller information the two sections into which this family is divided may be raised to the rank of separate families, yet the evidence brought forward by the writer mentioned above in favour of referring some of the genera to the Insectivora appears to be insufficient; no members of that order having more than three lower incisors or more than the normal three molars of the other Placental Mammals.[1] Considerable confusion has arisen in regard to the dentition of many of the members included in this family owing to the circumstance that in the mandible only one side of the teeth is generally seen, so that several genera have been made upon the evidence of remains of a few closely allied species. The clearing up of this confusion is mainly due to the careful observations of Professor Osborn. In this family all the genera are characterised by a channel on the inner side of the mandibular rami known as the *Mylohyoid groove* (fig. 1147)—a feature occurring in many recent Polyprotodonts. The number of lower incisors was probably always four (as in the modern *Didelphyidæ*), and the lower true molars are frequently in excess of that number, as in *Myrmecobius* alone among existing heterodont Mammals. These true molars may either consist of three or more cusps arranged in a single line, or they may be differentiated into a tritubercular blade followed by a posterior heel or talon. The premolars are very generally four in number, but they may be reduced to three, or perhaps two. Not unfrequently, as in the existing *Peramelidæ*, the root of the canine may be grooved.

[1] Judging from his latest memoir on the subject, it is probable that Professor Osborn would now considerably modify his views as to these divisions.

As a provisional measure this family may be divided into two groups or subfamilies, of which the first may be eventually raised to the rank of a distinct family. The first subfamily, or *Phascolotheriinæ*, is referred by Professor Osborn to his Prodidelphia, and is included in the *Triconodontidæ* (*infra*). The lower true molars consist typically of three main cusps arranged in a line, together

Fig. 1141.—Inner view of the right ramus of the mandible of *Phascolotherium Bucklandi*; from the Stonesfield Slate. Twice natural size. The outline figure is natural size. There should be a fourth incisor. (After Owen.)

with some accessory cusps; and it would appear that the upper molars were of similar structure. The lower incisors are separated from one another by intervals. The typical genus *Phascolotherium* (fig. 1141), from the Lower Jurassic slate of Stonesfield, in Oxfordshire, has the condyle of the mandible placed very low down; the lower dental formula is *I.* 4, *C.* 1, *Pm.* + *M.* 7, the canine is separated by a diastema from the first premolar, and the true molars have a well-marked cingulum on the inner side. *Amphilestes* (fig.

Fig. 1142.—Reversed inner view of the left ramus of the mandible of *Amphilestes Broderipi*; from the Stonesfield Slate. Twice natural size. The restoration of the anterior teeth is conjectural; and the condyle is placed too high. (After Owen.)

1142), from the same deposits, has a more numerous series of cheek-teeth, and a higher mandibular condyle. The exact dental formula is not known, although it may have been the same as in the undermentioned *Amblotherium*. The mandible from the same beds shown in fig. 1143 has been made the type of the genus *Amphitylus;* and according to Professor Osborn has teeth of the

same general type as those of the preceding genera. If this be so, it would appear to countenance the view that the present group should be separated from the *Amphitheriidæ*, but owing to the damaged condition of the specimen great caution is necessary in speaking positively as to the nature of the teeth.

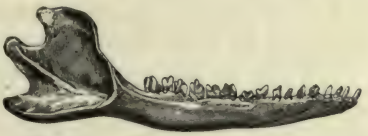


Fig. 1143.—Outer aspect of the right ramus of the mandible of *Amphitylus Oweni*; from the Stonesfield Slate. Enlarged. (After Owen.)

In the second subfamily, or *Amphitheriinæ*, the lower true molars are differentiated into a tritubercular anterior blade and a posterior heel or talon. Four premolars are present in all those genera of which the entire lower dentition is known; and the mandibular condyle is high. The upper molars are unlike the lower. Many of these genera are referred by Professor Osborn to his Insectivora Primitiva.

Before proceeding further some explanation is necessary as to the structure of this type of lower molar. Following the nomen-

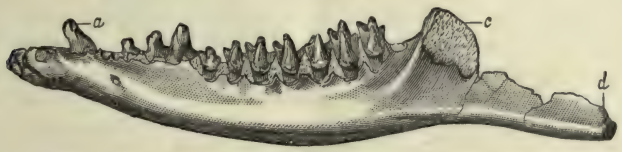


Fig. 1144.—Outer aspect of the left ramus of the mandible of *Dryolestes vorax*; from the Upper Jurassic of North America. Three times natural size. *a*, Canine; *c*, Coronoid process; *d*, Angle. The incisors and first premolar are absent. (After Marsh.)

clature adopted by Professor Flower the three cusps in the anterior half of such a "tritubercular" tooth may be collectively spoken of as the *blade* (fig. 1145, *a*, *b*, *c*); while the hinder part (*d*) may be termed the talon. In the blade the cusp *a* is termed the anterior,

Fig. 1145.—Upper, outer, and inner views of a left lower true molar of *Dasyurus*. *a*, Anterior cusp of blade (*paraconid*); *b*, Posterior cusp of do. (*protoconid*); *c*, Inner cusp of do. (*metaconid*); *d*, Talon (*hypoconid*).

the large one *b* the posterior, and the small one *c*, which is the innermost, the inner cusp. According to Professor Osborn these three cusps correspond to the three cusps of *Priacodon* (fig. 1147), and in both cases he applies to them the names of *para-*, *proto-*,

and *metaconid;* calling the talon of the present type the *hypoconid.* Corresponding terms ending in *cone* are applied to the upper molars of the same types.

It will be obvious that when a jaw is embedded in matrix with the inner surface exposed we shall only see the cusps *a* and *c* and the talon *d;* while when the outer surface is visible only the large cusp *b* will be observed. An example of the latter occurrence is shown in fig. 1146; and this circumstance has been the fruitful source of error in regard to a number of the Mesozoic types under consideration.

In the type genus *Amphitherium* of the Stonesfield Slate, or Lower Jurassic, the exact dental formula is unknown, but it may perhaps have been the same as in the next genus.[1] In *Amblotherium* (= *Peraspalax*, *Phascolestes*) of the Purbeck, or Upper Jurassic, of Dorsetshire, the lower dental formula is *I.* 4, *C.* 1,

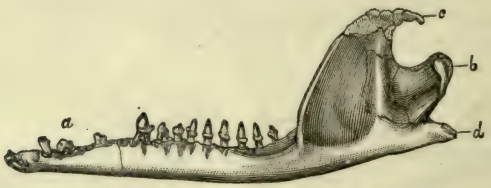


Fig. 1146.—Outer view of the left ramus of the mandible of *Amblotherium gracile;* from the Upper Jurassic of North America. Three times natural size. *a*, Canine; *c*, Coronoid process; *b*, Condyle; *d*, Mandible. (After Marsh.)

Pm. 4, *M.* (7–8), or the same as in the American Jurassic *Dryolestes* (fig. 1144). Several species are known, in some of which there were seven, and in others eight lower molars. The genus *Stylodon* has been founded upon the outer side of mandibles of *Amblotherium*, in which only the large posterior cusp (protoconid) of the blade of the molars is visible, as in the lower jaw shown in the accompanying woodcut, which has been made the type of the genus *Stylacodon*, of the Upper Jurassic of North America. The latter has eight lower molars, while the English form has only seven. *Achyrodon*, of the English Purbeck, is closely allied to *Amblotherium*, but differs in the form of the cusps of the molars. *Peramus* (*Leptocladus*) is a third Purbeck genus, with relatively stouter lower molars, in which Professor Osborn gives the lower dental formula as *I.* 3, *C.* 1, *Pm.* 6, *M.* 3. The North American *Dryolestes* has relatively shorter lower molars (fig. 1144), the woodcut clearly showing the three cusps of the blade and the talon of these teeth. *Asthenodon* and *Laodon* are other North American

[1] Professor Osborn regards it as *I.* ?, *C.* 1, *Pm.* 5, *M.* 6.

forms characterised by the small size of the talon of the lower molars; while the names *Dicrocynodon* (*Diplocynodon*), *Docodon*, and *Enneodon*[1] have been applied to more or less closely allied forms from the same deposits. Finally, Professor Osborn has given the name *Kurtodon* to certain upper jaws from the English Purbeck, which are probably referable to one or other of the above-mentioned genera. From the Laramie Cretaceous of North America Professor Marsh has described the remains of allied types. One of these has been termed *Didelphops* (*Didelophodon* or *Cimolestes*), while one tooth has been referred to the Jurassic genus *Dryolestes*, and another has been made the type of the genus *Pediomys*. The resemblance in the structure of the lower molars of the *Amphitheriinæ* to that of the corresponding teeth of *Dasyurus* and the *Didelphyidæ*, suggests that the latter have originated from an allied stock.

Family Spalacotheriidæ.—The genus *Spalacotherium*, with which *Peralestes* is identical, has a dentition which may probably be expressed by the formula $I.\ \frac{?}{3}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{4}{4}$, $M.\ \frac{6}{6}$. The true molars consist of a single column carrying three cusps, and thus corresponding to the blade of the tooth of the *Amphitheriinæ*. The reduction in the number of the lower incisors distinguishes this family from the last; but it is difficult to say whether the absence of the talon in the lower true molars is or is not a more specialised feature. The molars, which are of the typical tuberculo-sectorial type, approximate very closely in their plan of structure to those of the genus *Chrysochloris* among the Insectivora, but this cannot be taken as indicative that the present genus should be referred to that order, since a precisely analogous resemblance exists between the molars of *Tupaia* in the Insectivora and *Perameles* in the Marsupials. *Menacodon*, from the Upper Jurassic of North America, is an allied genus.

Family Triconodontidæ.—The last family of Mesozoic Mammals we have to consider is represented by the English Purbeck genus *Triconodon* (*Triacanthodon*), and the allied or identical *Priacodon* (fig. 1147) of the Upper Jurassic of North America. Professor Osborn includes in this family the *Phascolotheriinæ* already mentioned; but the reduction in the number of the incisors and the general *facies* of the teeth seems to indicate considerable difference—although the two groups are probably more or less nearly related. The mandibular condyle is placed still lower than in *Phascolotherium*, and apparently, indeed, than in any other known Mammal. The upper cheek-teeth resemble the lower. The dental formula in the mandible is *I.* 3, *C.* 1, *Pm.* 4, *M.* (3–4). The incisors were approximated, the cheek-teeth have

[1] Preoccupied, see page 1015.

an inner cingulum, and the molars consist of three subequal cones or cusps of a trenchant form, arranged longitudinally. There were apparently either three or four molars in different individuals of a single species. The fourth premolar was preceded by a milk-tooth resembling the true molars. It was considered by Sir R. Owen that the lower true molars of this genus corresponded to those of the existing *Thylacinus*, in which there is a bilobed blade and a talon. According, however, to Professor Osborn, this interpretation is incorrect; and that observer considers that the three cusps of the

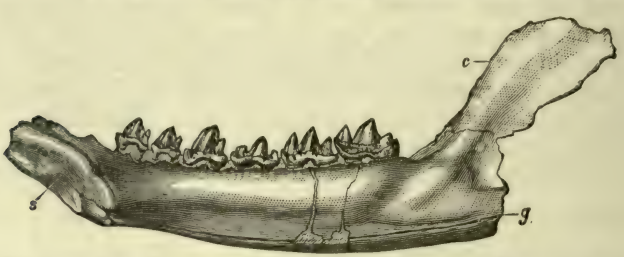


Fig. 1147.—Inner view of the left ramus of the mandible of *Priacodon ferox*; from the Upper Jurassic of North America. Three times natural size. *c*, Coronoid; *g*, Mylohyoid groove; *s*, Symphysis. The anterior teeth are wanting. (After Marsh.)

Triconodont type represent the three main cusps of the tooth of *Phascolotherium* (fig. 1141), and also correspond to the three lobes of the blade of the tritubercular molar of the *Amphitherium* type (fig. 1145); and he accordingly terms these three cusps the *para-*, *proto-*, and *metaconid*, and considers that the talon (*hypoconid*) is unrepresented.

Family Dasyuridæ.—With this family we come to the consideration of the existing Marsupials. The *Dasyuridæ* is an exclusively Australian family, comprising the largest known members of the suborder, and is divided into the subfamilies *Dasyurinæ* and *Myrmecobiinæ*. These are always $I.\ \frac{4}{3}$, $C.\ \frac{1}{1}$; but the number of cheek-teeth varies, although there are never more than three premolars. In the pes the hallux is usually either rudimental or absent, but the other four digits are well developed and subequal. In the *Dasyurinæ* the number of cheek-teeth does not exceed $\frac{7}{7}$, the upper true molars have triangular crowns, and those of the lower molars are differentiated into an anterior blade and a posterior talon (fig. 1145), like the lower carnassial tooth of many of the placental Carnivora of the present day. The mylohyoid groove may be present both in this and the next subfamily. The Tasmanian Wolf is the sole living representative of the genus *Thylacinus*, in

which the cheek-teeth number *Pm.* $\frac{3}{3}$, *M.* $\frac{4}{4}$, and the humerus has a foramen; but in the Pleistocene of Australia there occurs the considerably larger *T. spelæus*. *Sarcophilus*, of which the dentition is shown in fig. 1148, is also confined at the present day to Tas-

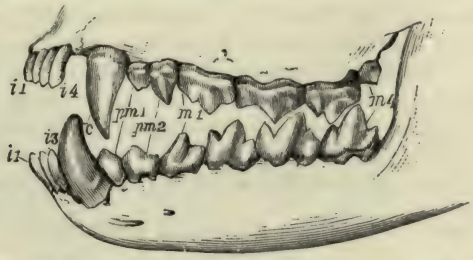


Fig. 1148.—Left lateral view of the dentition of *Sarcophilus ursinus*. Recent, Tasmania. *i*, Incisors; *c*, Canine; *pm*, Premolars; *m*, Molars. The tooth marked *pm* 2 is really *pm* 3.

mania, but a larger species inhabited the mainland of Australia in the Pleistocene. Indications of specialisation are shown by the reduction of the premolars to two, and also by the loss of the foramen in the humerus. The most generalised genus of the subfamily is *Dasyurus*, comprising several species of smaller size than the preceding. In the lower molars (fig. 1145) the blade has three cusps arranged in a triangle, and thus differs from those of *Thylacinus*, in

Fig. 1149.—*Myrmecobius fasciatus*, Australia. Reduced.

which the inner cusp is wanting. There is a mylohyoid groove in the mandible, and the humerus has a foramen. Species of *Dasyurus* at the present day range over the whole of the Australian continent, one of them dating from the Pleistocene. The subfamily *Myrmeco-*

biinæ is represented solely by the genus *Myrmecobius*. In this remarkable animal (fig. 1149) the lower incisors are separated from one another, the cheek-teeth number $\frac{8}{9}$, of which the first three in either jaw are premolars; while the molars have quadrangular multicuspidate crowns, and are not well differentiated from the premolars. Although some writers doubt the connection, it is probable that *Myrmecobius* is the direct descendant of forms closely allied to *Amphilestes*, of the Lower Jurassic of England; the relations of the two being perhaps somewhat similar to that existing between the living *Sphenodon* of New Zealand, and the more specialised *Hyperodapedon* of the English Trias.

Family Peramelidæ.—In this family, comprising the Bandicoots of Australia and New Guinea, the dental formula is *I.* $\frac{(4-5)}{3}$, *C.* $\frac{1}{1}$, *Pm.* $\frac{3}{3}$, *M.* $\frac{4}{4}$, and the pes has two of the digits reduced and connected by integument, as in the *Macropodidæ* among the Diprotodonts. Occasionally the canines have grooved or double roots. Remains of existing species of *Perameles* and *Peragale* occur in the Pleistocene of New South Wales.

Family Didelphyidæ.—In all the members of this family the dental formula is *I.* $\frac{5}{4}$, *C.* $\frac{1}{1}$, *Pm.* $\frac{3}{3}$, *M.* $\frac{4}{4}$. The incisors are very small and sharp; the canines are large; the premolars compressed; and the true molars constructed on the general plan of those of

Fig. 1150.—Left lateral view of the dentition of *Didelphys Azaræ*; South America. *i*, Incisors; *c*, Canine; *pm*, Premolars; *m*, True molars. The teeth marked *pm* 3 should be *pm* 4; the teeth between these and *pm* 1 being *pm* 2.

Dasyurus; the lower ones having a blade and talon, with a distinct inner cusp to the former. Each foot is furnished with five complete digits; and the humerus has an entepicondylar foramen. At the present day the Opossums, as the members of this family are commonly called, are confined to the New World, where they are represented by the genera *Didelphys* (fig. 1150) and *Chironectes*;

the latter being known only by a single species. Remains of existing species of both genera occur very commonly in the Pleistocene breccias of the Brazilian caves; and to the type genus may also be referred a large number of species from the Lower Miocene and Upper Eocene of Europe, which by some writers are referred to distinct genera under the names of *Peratherium* and *Amphiperatherium*. *Spalacodon*, of the Eocene of Hordwell, is probably a *Didelphys*. It was in *Didelphys Cuvieri*, of the Paris gypsum, that

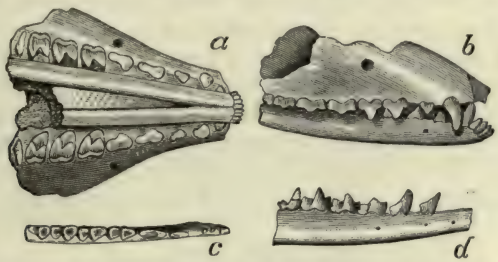


Fig. 1151.—*Didelphys* (?) *fugax*; from the White-river Miocene of Colorado. Twice natural size. *a*, *b*, Inferior and lateral views of skull; *c*, *d*, Superior and lateral views of right mandibular ramus. (After Cope.)

Cuvier demonstrated the existence of marsupial bones by a careful clearing of the matrix. Other extinct forms from the Miocene of North America (fig. 1151) may in all probability be referred to the same genus.

Suborder 2. Diprotodontia.—If we exclude the Multituberculata, which have been already mentioned, this suborder will be confined to the Australian region, where it has been known since the Pleistocene; and with this limitation it may probably be regarded as an offset from the more generalised Polyprotodontia. In all cases there is only a single pair of lower incisors, but in the upper jaws there are usually three pairs of such teeth, although they are reduced to one in the Wombats. The lower incisors, and the first, or innermost, pair of upper incisors are always of large size and adapted for cutting. The canines are frequently absent, and when present are of relatively small size. The crowns of the true molars are either tuberculate or have transverse ridges; and as a general rule there are not more than two premolars. Very frequently the last premolar has a long and narrow crown, with a concave superior border adapted solely for cutting.

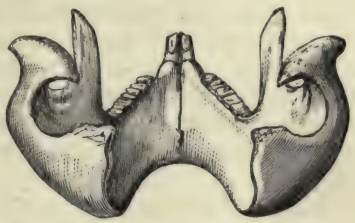


Fig. 1152.—Posterior reduced view of the mandible of the Wombat (*Phascolomys*).

Family Phascolomyidæ.—This family is now represented only by the genus *Phascolomys*, or Wombats; in which the dental formula is $I.\ \frac{1}{1}$, $C.\ \frac{0}{0}$, $Pm.\ \frac{1}{1}$, $M.\ \frac{4}{4}$, and all the teeth grow from persistent pulps. The true molars have curved crowns consisting of two subequal lobes, while the premolar has only a single lobe, and is not preceded by a milk-tooth. The mandible (figs. 1152, 1153) is characterised by having a pit and perforation in the masseteric fossa. The fore and hind limbs are of equal length, the former being of great strength in accordance with the fossorial habits of the genus; and the humerus has a foramen. There are five digits in the manus, all of which are provided with long curved claws, and are of subequal size; but in the pes the hallux is imperfect, and the three middle digits are of nearly equal size, and partly enclosed in a common integument. Three existing species of Wombat are known, which are divided into two groups according to the char-

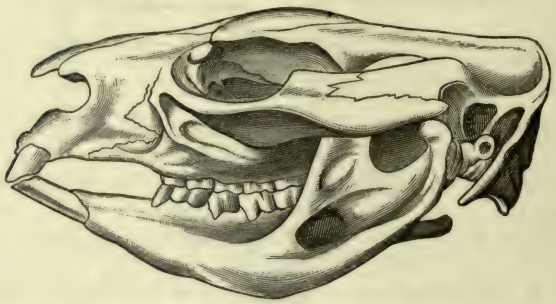


Fig. 1153.—Left lateral view of skull of Wombat (*Phascolomys latifrons*). Reduced. Australia.

acters of the skull and teeth; none of them being of large size. In the Pleistocene of Australia we meet with remains not only of these existing species, but also with several extinct types, one of which was of considerably larger dimensions. In the same deposits are also found remains of the extinct genus *Phascolonus* (with which the so-called *Sceparnodon* appears to be identical), characterised by certain peculiarities in the incisors. The one known species probably attained the dimensions of a Tapir, although of considerably stouter build.

Family Nototheriidæ.—This family is represented only by a single definitely known genus from the Australian Pleistocene described as *Nototherium*.[1] This includes one (or possibly more) large

[1] It has recently been suggested that the figured skull does not belong to *Nototherium*, and that it should be termed *Zygomaturus;* but this view is not sup-

species, and appears to have been allied in many respects to the Wombats, although presenting several of the dental characters of the next family. The dental formula is $I.\ \frac{3}{1}$, $C.\ \frac{0}{0}$, $Pm.\ \frac{1}{1}$, $M.\ \frac{4}{4}$; and it appears that, at least normally, there was no deciduous milk-molar. The cheek-teeth are rooted; the crowns of the true molars carrying two simple transverse ridges. The cranium (fig. 1154) presents a very singular contour, the nasals being transversely expanded; and the mandible differs from that of the *Phascolomyidæ*

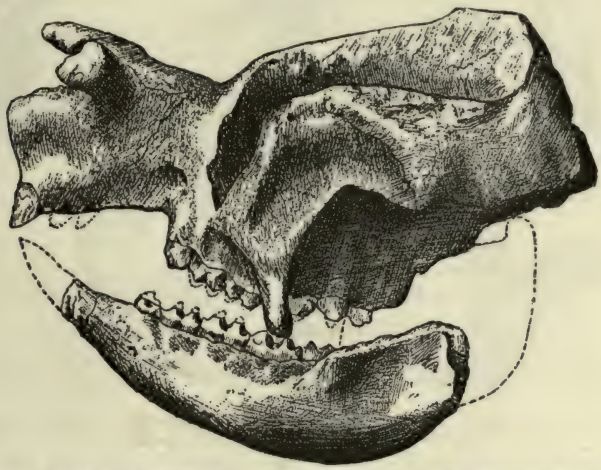


Fig. 1154.—Left lateral view of the skull of *Nototherium Mitchelli*; from the Pleistocene of Australia. One-sixth natural size. (After Owen.)

by the absence of a pit or perforation in the masseteric fossa (fig. 1154). The limb-bones appear, however, to have resembled those of the latter family; the humerus having a distal foramen, and being evidently adapted for fossorial habits, although it is difficult to believe that an animal of such comparatively large bulk could have lived in burrows.

Family Diprotodontidæ.—The genus *Diprotodon*, of the Australian Pleistocene, is the sole representative of this extinct family, and the type species (fig. 1155) is the largest known member of the order; its bulk being fully equal to that of a large *Rhinoceros*. The dental formula is the same as that of *Nototherium*; and the structure of the cheek-teeth of the two genera is also very similar, although the lower true molars of *Diprotodon* have no median longitudinal bridge. In the incisors of this genus the first pair are

ported by sufficient evidence. A small Nototheroid from Queensland has received the preoccupied name *Owenia*.

scalpriform, and grow from persistent pulps. The fore and hind limbs are of approximately equal length, and adapted solely for walking; the humerus has no foramen; and it is probable that the covering of the toes approximated to the nature of hoofs. The mandible, although more convex below, is not unlike that of *Nototherium*. Professor Huxley has named a second species on the

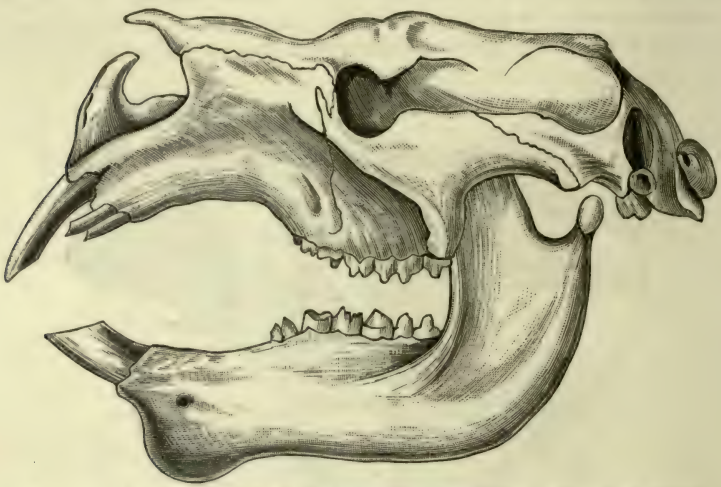


Fig. 1155.—Left lateral view of the skull of *Diprotodon Australis*; from the Pleistocene of Australia. Much reduced. (After Owen.)

evidence of premolars, but it is not certain that this determination is correct.

Family Phalangeridæ. — This family includes the existing Phalangers and the Koala (*Phascolarctus*), as well as a remarkable extinct genus. All these animals have *I.* $\frac{3}{1}$, and an upper and frequently also a minute lower canine; while the premolars may vary from $\frac{2}{1}$ to $\frac{3}{3}$, and the true molars from $\frac{1}{2}$ to $\frac{4}{4}$. The structure of the cheek-teeth is subject to great variation in the different genera; the fourth premolar being either secant or tubercular. There is no pit or perforation in the masseteric fossæ of the mandible. The limbs are of nearly equal length; the manus has five subequal digits, but the second and third digits of the pes are very slender and partially united by integument; and the hallux is always opposable. In many of the true Phalangers the fourth premolar is grooved, and the dentition closely resembles that of the existing genus *Hypsiprymnodon* among the *Macropodidæ*. Of living genera the only one

known to occur in a fossil state is *Pseudochirus*, of which the remains of an existing species are found in the Pleistocene cave-deposits of New South Wales. The most interesting member of the family is, however, the large Pleistocene *Thylacoleo* (fig. 1156), which forms the type of a distinct subfamily. The dentition may be represented by the formula $I.\frac{3}{1}$, $C.\frac{1}{0}$, $Pm.\frac{3}{3}$, $M.\frac{1}{2}$. The true molars and earlier premolars were small, and more or less functionless, while the fourth premolar is enormously developed, and has a long sharp cutting-edge, so that, in union with its fellow of the opposing jaw,

Fig. 1156.—Right lateral view of the skull of *Thylacoleo carnifex;* from the Pleistocene of Australia. One-fifth natural size.

it forms a cutting instrument of extraordinary power. In originally describing this remarkable animal from fragments of jaws containing the fourth premolar, Sir Richard Owen came to the conclusion that the structure of this tooth indicated a carnivorous animal adapted to prey upon the huge Diprotodons and Nototheres; but the discovery of the complete skull has shown that the animal was more closely allied to the existing Phalangers, and that it could not have possessed the destructive habits attributed to it by its describer, although it is quite probable that its diet may have included the smaller mammals, birds, and eggs. It was at one time considered that the Multituberculata were allied to this genus.

Family Macropodidæ.—The last, and in many respects the most specialised family of the Diprotodontia includes the Kangaroos, Wallabies, and Kangaroo-rats. The dentition is represented by the formula $I.\frac{3}{1}$, $C.\frac{(0-1)}{0}$, $Pm.\frac{2}{2}$, $M.\frac{4}{4}$. The incisors are extremely secant, those of the mandible being frequently movable against one another. The premolars may have either triangular or cutting crowns, and in the latter case (fig. 1158) are frequently grooved; the third premolar is always, and the fourth in some cases,

deciduous, the latter being invariably preceded by a milk-tooth. The true molars have either four tubercles or two transverse ridges, and frequently an anterior talon. The mandible has a deep pit and perforation in the masseteric fossa. The pectoral limb is always more or less markedly shorter than the pelvic. The manus is provided with five subequal digits; but in the pes (fig. 1157) the hallux is generally absent, the second and third digits being very minute and enclosed in a common integument (*syndactylous*), while the fourth is greatly enlarged, and forms the main base of support. The majority of forms progress by making enormous leaps by means of their powerful hind-limbs; but a few, like *Dendrolagus* of New Guinea, are arboreal. This family may be divided into three subfamilies. In the first, or *Hypsiprymnodontinæ*, there is a distinct hallux, and the dentition closely resembles that of the *Phalangeridæ;* the fourth premolar being small, obliquely grooved, and directed inwardly at its anterior border. In the small existing *Hypsiprymnodon* there is no tooth between the lower incisor and the fourth premolar; but in a large extinct form from the Pleistocene of New South Wales, described under the name of *Triclis*, there is a minute tooth behind the lower incisor corresponding to the tooth in the *Phalangeridæ* commonly reckoned as the representative of the canine. This genus, therefore, forms an important link between the last-named and the present family. In the second subfamily, or *Potoroinæ*, the hallux is absent; the first upper incisor is narrower and longer than either of the others (fig. 1158); there is always an upper canine; the fourth upper premolar is elongated and secant, and usually with the grooves strongly marked; while the true molars are tuberculate, with the fourth smaller than the third. The Kangaroo-rats are divided into the genera *Potorous* (*Hypsiprymnus*), *Bettongia*, and *Æpyprymnus;* the latter being represented in the Pleistocene of New South Wales by remains of the existing species.

Fig. 1157. — Dorsal aspect of the right pes of *Macropus Bennetti*. Reduced. (After Flower.)

The third subfamily, or *Macropinæ*, is distinguished from the last by the following characters: The cutting-edges of the upper incisors form nearly a straight line (fig. 1159); the upper canine is usually either absent or very small; and the fourth premolar, which may be shorter or longer than the first true molar, has either an inner basal ridge or lobe. In the existing genus *Macropus* (Kangaroos) the fourth upper premolar has a sharp cutting outer edge, and an inner ridge or tubercle; and this tooth in both jaws may be either longer or shorter than the first true molar. The two rami of the mandible

are not anchylosed together, and the hind-limbs are much longer than the front ones. A large number of fossil species occur in the Australian Pleistocene, among which may be mentioned several very large forms like *M. brehus*, which have the fourth premolar longer than the first true molar, and are allied to the small existing Wallaby, *M. ualabatus* (which also occurs in the Pleistocene).

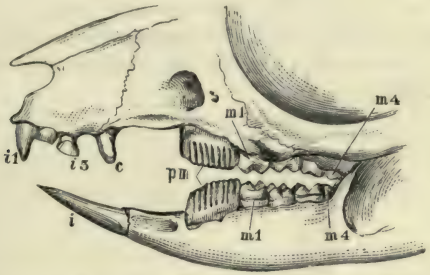


Fig. 1158.—Dentition of *Potorous*. *i*, Incisors; *c*, Canine; *pm*, Premolar; *m*, Molars.

Then, again, we have in the same deposits remains of the existing Rock-Kangaroo, *M.* (*Petrogale*) *penicillatus*, and also of the larger *M. robustus*, and some allied extinct forms. Another group, in which the fourth premolar is very small and soon falls out, is represented by the existing *M. giganteus*, and the larger extinct *M. titan* and *M. ferragus*. *Sthenurus* is an entirely extinct genus characterised by the presence of a distinct inner lobe to the fourth upper premolar, and is represented by a single species of considerable size. In *Procoptodon*, again, which is likewise extinct, the fourth

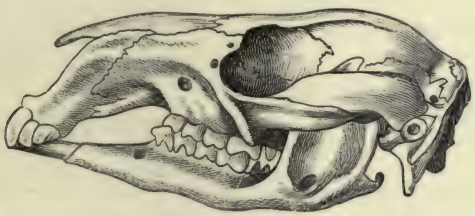


Fig. 1159.—*Macropus Bennetti*. Lateral view of skull; from Australia. Reduced.

upper premolar is like that of *Sthenurus*, but the rami of the mandible become anchylosed together in the adult; more than one species are known. Finally, the extinct *Palorchestes*, comprising the largest known member of the family, is distinguished from the last-named genus by the longer mandibular symphysis, and the absence of an anterior talon in the upper true molars. The length

of the skull of the one known species is estimated at as much as sixteen inches.

Of Uncertain Ordinal Position.—Here may be conveniently noticed some minute Mammals, mostly known by teeth or fragments of jaws, from the Lowest Eocene of Rheims, of which it is difficult to say whether they are Marsupial or Placental, although it is highly probable that some of them belong to the former division. Among these may be mentioned *Tricuspodon*, with teeth resembling those of *Spalacotherium ;* the allied *Orthaspidotherium* and *Pleuraspidotherium ;* and *Procynictis*, in which the true molars approximate to those of *Amblotherium*.

CHAPTER LX.

CLASS MAMMALIA—continued.

Orders Edentata, Cetacea, and Sirenia.

Subclass II. Eutheria.—The whole of the remaining orders of Mammalia are grouped together in a single subclass,[1] which is characterised by the fœtus being nourished *in utero* by means of the maternal blood passing through an allantoic placenta. This subclass is sometimes termed the Placentalia, but more generally the Eutheria. Throughout this subclass the urinogenital organs are provided with an external aperture quite distinct from that of the alimentary tube; the corpus callosum of the brain is well developed; there is never any marked inflection of the angle of the mandible; and distinct epipubic bones are absent in the pelvis. With the exception of the three orders forming the subject of the present chapter, the dental formula can always be reduced to some modification of that given on page 1249. At the present day the various orders have become so well differentiated as to render their definition comparatively easy; but fossil forms indicate such a close connection between the majority of them, that such definition becomes frequently a matter of extreme difficulty, if not an absolute impossibility; and it is to be remembered that it is entirely due to our non-acquaintance with forms which must have once existed that renders even these imperfect definitions practicable.

There is at present no conclusive evidence of the existence of any member of this subclass previous to the Eocene.

Order III. Edentata.—The Edentata are widely different from all other existing Mammals, although there are indications of affinity to certain extinct forms mentioned in the sequel under the heading of the Tillodontia. Almost the only common character presented by the various existing members of this order is that the teeth, when

[1] It has, indeed, been proposed to form a separate subclass—Paratheria—for the reception of the Edentates.

present, are devoid of enamel, are never developed at the extremities of the jaws in the situation of the incisors of other Mammals, and are always homœodont and grow from persistent pulps; while, with the exception of one genus of the *Dasypodidæ*, they are likewise monophyodont. It has, however, been recently observed by Dr Ameghino that enamel was present in the teeth of certain South American fossil forms; while in the genus *Diadomus*, from those deposits, a pair of canine-like teeth occur in the symphysis of the mandible. In many of the genera the teeth are simply cylindrical, but they may be transversely ridged, and occasionally they have a very complex internal structure. Not unfrequently the maxillary bone sends down a large descending process in the zygomatic arch (fig. 1163 *bis*); and certain members of the order are remarkable as being the only known Mammals which develop a bony exoskeleton. The cervical vertebræ are short and wide, with nearly flat terminal faces to their centra.

The distribution of the Edentates is very restricted. In Europe neither at the present day nor in past times is there any known representative of the order; the so-called *Macrotherium* being now known to be identical with the Ungulate genus *Chalicotherium*, while *Ancylotherium* is also allied to the latter. In tropical Asia we find the Pangolins or *Manidæ;* and in Africa the *Orycteropodidæ*. South America is, however, the headquarters of the order, which is there represented at the present day by the Anteaters, the Sloths, and the Armadillos, and in past epochs by the huge Ground-Sloths and the Glyptodonts. The gigantic size of these fossil forms as compared with their existing allies of the same area is paralleled by the instance of the fossil Diprotodont Marsupials of Australia.

It is evident that the Edentates are widely separated from all other existing Eutherians; and Professor W. K. Parker, in view of the tendency to a variation in the number of cervical vertebræ and other features, has suggested a separate origin from a Prototherian stock. Professor Cope, however, looks upon the order as allied to the Tillodonts, and the occurrence of enamel in the teeth of some fossil forms may support this view.

Family Orycteropodidæ. — The Ant-Bears (*Orycteropus*) of Africa are characterised by the body being covered merely with a few hairs; and by the numerous teeth, which are of a remarkably complex structure, owing to the presence of a number of vertical pulp-canals. In the fore-limb the pollex is absent, but the hind-limb has five digits. The femur has a third trochanter, and the terminal digits are provided with moderate-sized claws, suitable for digging the burrows in which these creatures dwell. At the present day *Orycteropus* is mainly characteristic of the Ethiopian region, although one of the two species ranges into Egypt. Till very re-

cently nothing was known of the palæontological history of the family, but Dr Forsyth-Major has recorded a species from the Lower Pliocene of the isle of Samos, in the Turkish Archipelago, distinguished from the existing species by the larger size of the lateral

Fig. 1160.—Lateral view of the skull of *Orycteropus capensis*. Africa. Reduced.

metatarsals. The occurrence of this species seems to point to the conclusion that Asia was the original home of the family.

Family Manidæ.—The Pangolins (*Manis*) of India and Africa are distinguished from all other Mammals by the body being covered superiorly with a coat of imbricated, horny, epidermal scales. Teeth are absent; the limbs are short and furnished with five digits, of which the terminal claws are long, curved, and bifid at the extremities. The humerus has an entepicondylar foramen, but there is no third femoral trochanter, and clavicles are wanting. The large *Manis gigantea* of Western Africa is found in a fossil state in the Pleistocene cave-deposits of Southern India; while in the Lower Pliocene of the isle of Samos we have a species three times the size of the latter, which has been made the type of the genus *Palæomanis*. A phalangeal from the Indian Siwaliks described as *Manis* appears to belong to *Chalicotherium*.

Family Dasypodidæ.—The Armadillos (fig. 1161) of South America are characterised by the presence of a bony dorsal carapace, composed of a series of dermal scutes, of which a certain number are always arranged in movable bands, while the others may be articulated together into solid scapular and pelvic bucklers, as in fig. 1161. The frontal region of the skull also has a buckler; while the tail is defended by rings or tubercles of bone. In the existing genera the teeth are simply conical; and in *Tatusia* all except the last have milk predecessors. Many of the cervical vertebræ are anchylosed together; and the stout humerus has an entepicondylar foramen, and the femur a third trochanter. The fore-feet are provided with very strong curved claws; and, like the *Manidæ*, the existing forms are of burrowing habits. The Pleistocene cave-deposits of Brazil yield remains of some existing and some extinct

species of the genera *Dasypus*, *Tatusia*, *Tolypeutes* (fig. 1161), and *Xenurus*. In the Pleistocene of Argentina we meet with a large extinct type known as *Eutatus*, which is characterised by the whole of the carapace consisting of movable bands, which are thirty-three in number. The Tertiaries of the same region have also yielded a much larger form known as *Dasypotherium*, which appears to connect the living forms with the next genus. There were eight lower teeth, of which the second appears to have been enlarged, as in some species of *Mylodon*. The most remarkable genus is, however,

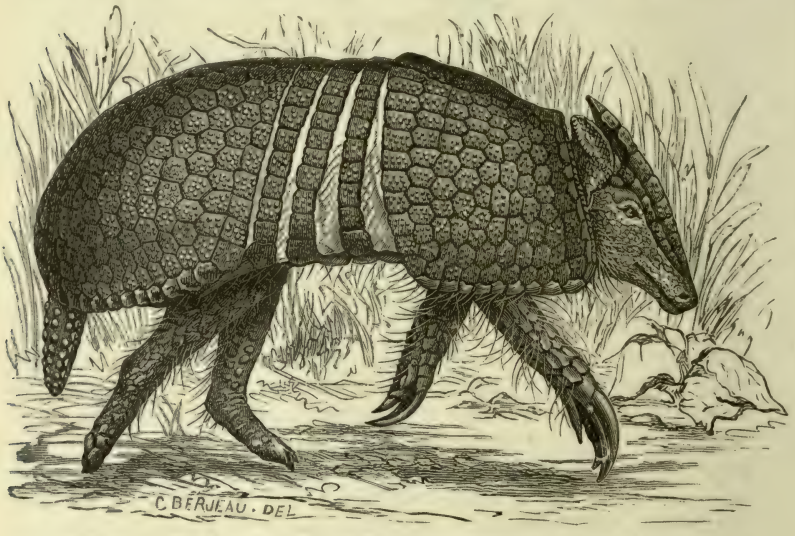


Fig. 1161.—The three-banded Armadillo (*Tolypeutes conurus*). South America. One-third natural size. (After Murie.)

Chlamydotherium, of the South American Pleistocene, in which the teeth approximate in structure to those of the next family. The carapace has several movable bands; and the largest species is considered to have equalled the bulk of a Rhinoceros. The existing Armadillos are therefore dwarfs by the side of these huge allies of an earlier epoch.

Family Glyptodontidæ.—In this extinct American family the body was covered by a carapace as in the Armadillos; but this carapace (fig. 1162) has no movable bands, so that the animal could not roll itself up; and since the fore-feet have short thick toes, it is evident that the habits of this group were not fossorial. The carapace usually has its component scutes united by suture, but in one genus they were separate; the scutes are, moreover, usually ornamented with a sculpture, which varies in the different

genera and species; but they may be either plain or tuberculated. There is usually a ventral buckler (never found in the Armadillos),

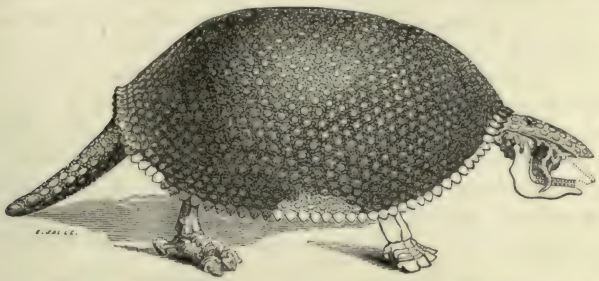


Fig. 1162.—*Glyptodon clavipes;* Pleistocene, South America. Reduced greatly. The tail is incorrectly restored, and it is probable that the figured portion belongs to *Hoplophorus.*

and the tail is enclosed in a complete bony sheath. The teeth are $\frac{8}{8}$ in number, and have two deep grooves on either side dividing them into three nearly distinct lobes (fig. 1163); the generic name being derived from this grooving or fluting. The facial part of the cranium is characterised by its extreme shortness (fig. 1163 *bis*); and there is a long descending maxillary process in the zygomatic arch. Nearly the whole of the vertebral column is anchylosed into a long tube, but there is a complex joint at the base of the neck. This family is mainly characteristic of South America; but species of *Glyptodon* ranged as far as Mexico and Texas into North America. Great confusion has arisen in respect to the classification of the Glyptodonts, owing to the difficulty of referring isolated caudal sheaths to their proper carapaces. The forms with a solid carapace may, however, be arranged as follows. In *Hoplophorus* the scutes of the carapace are sculptured, and often comparatively thin, the peripheral series being flat; while the caudal sheath has several movable rings, and terminates in a long

Fig. 1163.—Grinding surface of two teeth of *Glyptodon reticulatus;* from the Pleistocene of South America.

Fig. 1163 *bis.*—Left lateral view of the skull of *Glyptodon;* from the Pleistocene of South America. One-tenth natural size. (After Burmeister).

subcylindrical tube (fig. 1164), ornamented with a number of large disks, surrounded by a series of much smaller ones. It is considered probable that the caudal tube represented in fig. 1162 belongs to this genus. The humerus has an entepicondylar foramen, and there are four complete digits to each foot. An allied form, from the infra-Pampean of Patagonia, has received the name of *Palæhoplophorus;* while the terminal tube of a caudal sheath from Uruguay has been made the type of the genus *Eleutherocercus*. The latter specimen is characterised by its loose attachment to the enclosed vertebræ, and by the great number of perforations for bristles, so that the tail of the living animal must have resembled a huge bottle-brush. The genus *Panochthus* is characterised by the

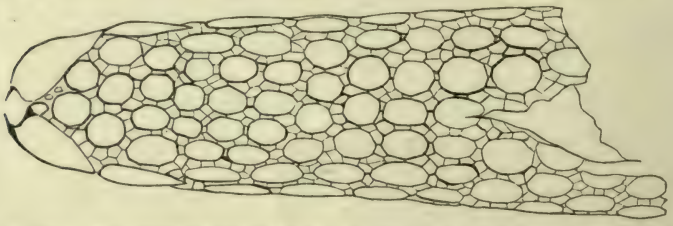


Fig. 1164.—The incomplete terminal tube of the caudal sheath of *Hoplophorus*; from the Pleistocene of South America. One-third natural size.

excessive thickness of its carapace, the scutes of which are tuberculated, and by a caudal sheath composed proximally of several movable rings, but terminating in a long compressed tube ornamented with tubercles, of which some were of very large dimensions, and marked with a radiate sculpture. In *Euryurus* the caudal sheath is of somewhat similar type, but the scutes of the carapace are simply rugose. *Dædicurus*, again, also has the scutes of the carapace rugose, but the terminal tube of the caudal sheath is enlarged into a flattened club-like expansion, covered with coarse tubercles, interspersed with a few larger rough disks having a radiate sculpture; these disks having probably been surmounted, as in *Panochthus*, with horny epidermal spines. The type species attained a length of about 12 feet. Finally, in *Glyptodon* (fig. 1162), with which *Schistopleurum* is probably identical, the scutes of the carapace had a rosette-like sculpture, the peripheral ones being raised into conical prominences, and the caudal sheath, at least in several species, was entirely composed of a series of movable rings, ornamented with large conical tubercles. The humerus was devoid of an entepicondylar foramen; and while there were five complete digits in the manus, those of the pes were reduced to four. *Thoracophorus* differs from all the foregoing in having the scutes of the carapace separated from one another, and thereby approximates

to some of the *Megatheriidæ*, in which there were a number of small ossicles embedded in the dermis of the dorsal region. A similar condition prevails in *Carioderma*, of the Loup-Fork beds of Texas.

Family Myrmecophagidæ.—This family comprises the true Ant-eaters of South America, represented by the genera *Myrmecophaga*, *Tamandua*, and *Cycloturus;* but appears to be unknown in a fossil state. The jaws are entirely destitute of teeth; the body is clothed with hair; the tail is long; there are either four or five digits in the pes; and the third digit of the manus is the longest.

Family Megatheriidæ.—The members of this family are entirely extinct, and are confined to the New World. They comprise a number of very large forms adapted solely for walking on the ground, and showing in their skeletal organisation characters intermediate between the preceding and the following families. Thus, while their vertebræ and limbs are constructed like those of the *Myrmecophagidæ*, their crania and dentition resemble those of the

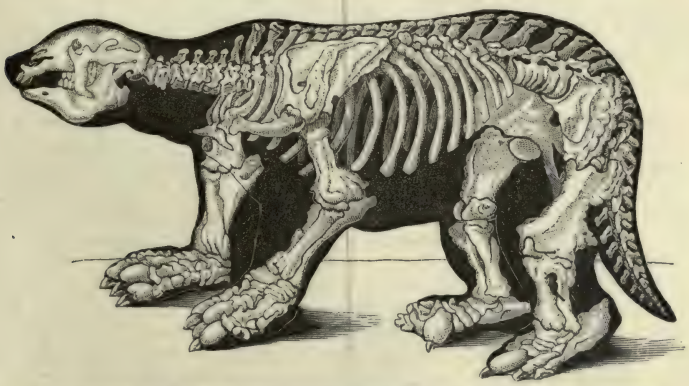


Fig. 1165.—*Megatherium americanum;* from the Pleistocene of South America. Much reduced.

Bradypodidæ. One species of the genus *Scelidotherium* approximates, however, in cranial characters to the former family; and it is probable that the whole three families have originated from a single stock. The number of the teeth is usually $\frac{5}{4}$; and the first and second teeth may be either in apposition or separated by an interval. The femur has no third trochanter; and the under surface of the odontoid process of the axis vertebra presents a peculiar flattened surface for articulation with the atlas. The type genus *Megatherium*[1] is found in the Pleistocene of both South and North

[1] This name should properly be *Megalotherium*, but its antiquity renders it somewhat sacred.

America ; the typical *M. americanum* (fig. 1165) of the former region being fully equal in bulk to the largest species of Rhinoceros. The teeth (fig. 1166) consist of square prisms, wearing into transverse ridges through the presence of two vertical plates of hard dentine intercalated between softer dentine and cement ; they are similar in

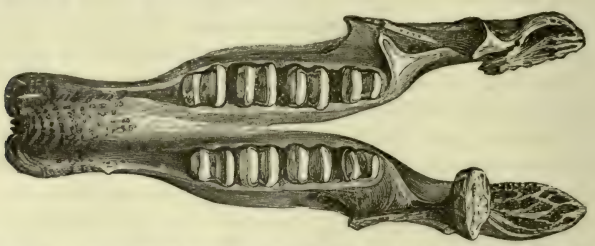


Fig. 1166.—*Megatherium americanum*.—Oral surface of the mandible ; from the Pleistocene of Buenos Ayres. Reduced.

structure, and are all in contact. The feet are provided with powerful and huge claws, the third digit in each foot being the longest ; and the humerus has no foramen.

There are indications that the snout was prolonged, and more or less flexible ; and the tongue was probably prehensile. From the characters of the molar teeth it is certain that the Megathere was purely herbivorous in its habits ; and from the enormous size and weight of the body it is equally certain that it could not have imitated its modern allies, the Sloths, in the feat of climbing, back downwards, amongst the trees. It is clear, therefore, that it sought its sustenance upon the ground, and it was originally supposed to have lived upon roots ; but by a masterly piece of deductive reasoning, Sir R. Owen showed that this great Ground-sloth lived upon the foliage of trees, like the existing Sloths—but with this difference, that instead of climbing amongst the branches, it actually uprooted the tree bodily. In this *tour de force*, the animal sat upon its huge haunches and mighty tail, as on a tripod, and then grasping the trunk with its powerful arms, either wrenched it up by the roots or broke it short off above the ground. Marvellous as this may seem, it can be shown that every detail in the skeleton of the Megathere accords with the supposition that it obtained its food in this way.

A smaller but allied form from the Pleistocene of South America has been named *Oracanthus*, but since this term is preoccupied by a genus of Palæozoic Fishes, it should be changed. The genus *Scelidotherium* (fig. 1167), which may be taken to include *Platyonyx*, and likewise occurs in the South American Pleistocene, comprises a number of species, and has characters in some respects intermediate between the preceding and the following genera. The teeth in the upper jaw have an irregularly oval section, while those of the mandible are usually subtriangular ; the whole of the series are in contact, and their crowns do not wear into ridges. The

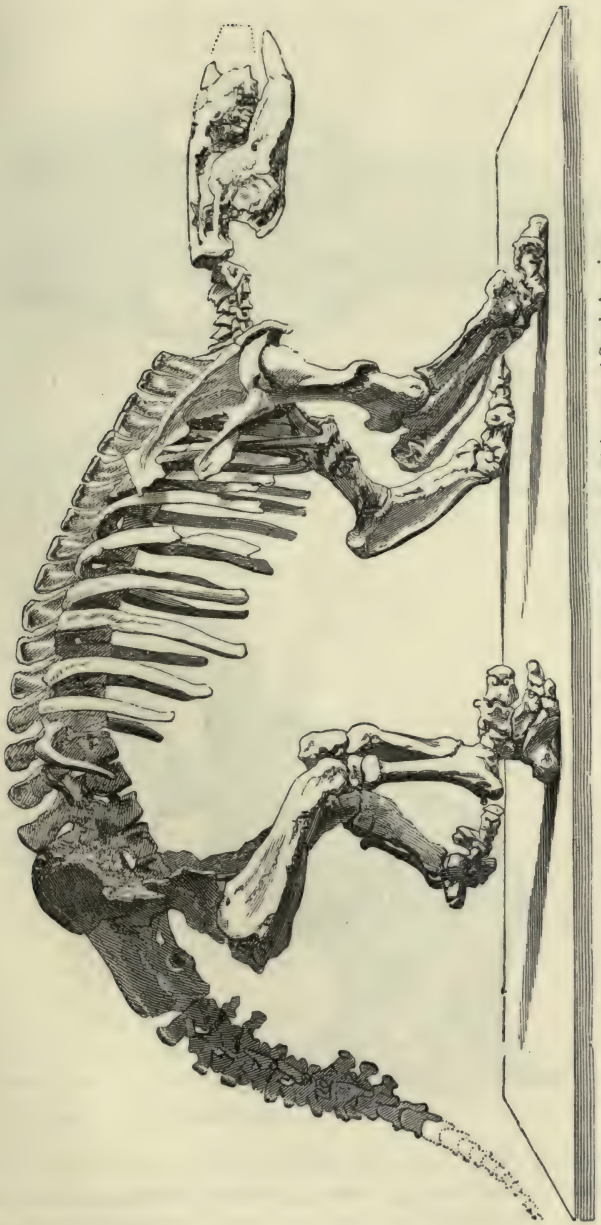


Fig. 1167.—The imperfect skeleton of *Scelidotherium*; from the Pleistocene of South America. One-sixteenth natural size. (After Capellini.)

cranium is low and elongated; and, especially in the type species (fig. 1168), approximates to that of the *Myrmecophagidæ*. The length of the nasals is subject to great variation in the different

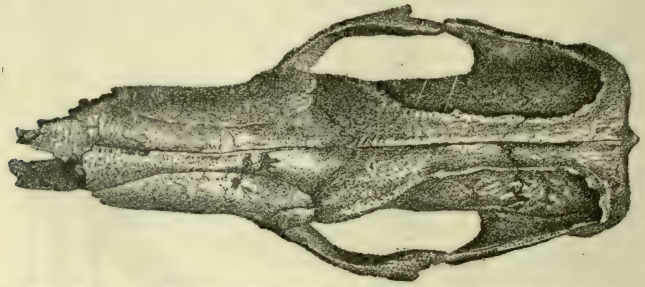


Fig. 1168.—Frontal aspect of the cranium of *Scelidotherium leptocephalum*; from the Pleistocene of South America. One-sixth natural size.

species. The structure of the feet shows a marked deviation from that of *Megatherium*; and the humerus was usually provided with a foramen. The figure of the skeleton is taken from a specimen in the museum at Bologna. The genus *Mylodon* (fig. 1169) com-

Fig. 1169.—*Mylodon robustus*; from the Pleistocene of South America. Much reduced.

prises another group of large Ground-Sloths, which has been split up by some writers into the genera *Lestodon*, *Pseudolestodon*, *Grypotherium*, &c., according to certain not very important differences in

the structure and mode of arrangement of the teeth. In the upper jaw the teeth are usually subtriangular or oval in transverse section, and in typical species there is only a short interval between the first and second tooth in each jaw, and the former is worn horizontally; but in other species there is a considerable interval between the two, and the first is worn obliquely, as in certain Sloths. The humerus has no entepicondylar foramen; and in the shortness of the skull and the characters of the teeth this genus approaches nearer to the modern Sloths than any other member of the family. The best known species is the South American *Mylodon robustus* (fig. 1169), which was smaller than *Megatherium americanum*, its length being about 11 feet; but *M. armatus* (the type of the so-called *Lestodon*), from the same country, is considerably larger. The type species is *M. Harlani*, from the Pleistocene of "Big-bone Lick," in Kentucky, North America; while the Patagonian *M. Darwini* is a very aberrant form, regarded by some writers as generically distinct, and named *Grypotherium*. There are numerous small dermal scutes, which do not articulate with one another. *Megalonyx*, from the Pleistocene of North America, is an allied genus, characterised by the long interval between the large first and the smaller second tooth, and also by the presence of an entepicondylar foramen to the humerus. The type species is *M. Jeffersoni*, from Kentucky and Tennessee; while *M. cubensis*, from the Pleistocene of Cuba, has been separated by some writers under the name of *Megalochnus* (*Myomorphus*). Another form hitherto known as *Cælodon*, but which may be named *Nothrotherium*, on account of the preoccupation of the former term, occurs in the Pleistocene cave-deposits of Brazil, and agrees with *Megalonyx* in the structure of its limbs, but has teeth of the type of those of *Megatherium*, although their number is reduced to $\frac{4}{3}$; the type species considerably exceeded in size the largest Ant-eater of the present day.

The Mammals from the Lower Pliocene and Miocene of North America which have received the names *Moropus* and *Morotherium*, and are regarded by Professor Marsh as forming the type of a distinct family of Edentates—the *Moropodidæ*—probably belong to the Ungulate family *Chalicotheriidæ*.

Family Bradypodidæ.—This family is entirely confined to South America, and now comprises two genera of comparatively small animals which are of exclusively arboreal habits. The body is clothed with coarse hair; the teeth are $\frac{5}{4}$ in number in each jaw, and are of subcylindrical form, with a central axis of soft dentine,

surrounded by a coat of a harder kind of the same substance. The fore-limbs are enormously elongated; and both the manus and pes are furnished with long, curved claws; the number of digits never exceeding three in each foot. The skull (fig. 1170) is short, with a descending maxillary process to the zygoma; and the tail is rudimentary. In *Bradypus* (fig. 1170) the first tooth is equal in size to the second, and is worn horizontally; while the digits are reduced to two. In *Cholœpus*, however, the first tooth is considerably larger than the second, from which it is separated by a much longer interval than in *Bradypus*, and wears obliquely; while there are three digits to each foot. The only known fossil form is from the

Fig. 1170.—Skull of *Bradypus gularis*. Recent. South America. Reduced.

Pleistocene of Argentina, and has been named *Nothropus priscus*; it appears to have been about twice the bulk of *Bradypus didactylus*, and has the first lower tooth separated by a very long interval from the second, although it is of smaller size; the cranium, upper dentition, and feet are unknown.

Order IV. Cetacea.—The Cetacea form, perhaps, the most readily defined and sharply differentiated order in the whole class. Their contour is fish-like, the body being fusiform, and passing imperceptibly into the head without any distinct external neck, and posteriorly gradually tapering to the extremity of the tail, which is furnished with a pair of horizontally-expanded "flukes," formed of dense fibrous tissue covered with skin (fig. 1178). The head is frequently very large, and may be as much as one-third the total length of the animal. The pectoral limbs are reduced to ovoid, paddle-like, organs; and there are no external traces of pelvic limbs. The skin is smooth and without hair; although bristles may be present in the neighbourhood of the mouth, more especially in young individuals. Frequently there is a median dorsal fin (fig. 1178), which however has no bony supports. Both the eye and the external auditory aperture are small; the former having no nictitating membrane, and the latter no pinna. The nostrils open by a single

or double aperture usually near the vertex of the skull. The bones are usually of a spongy nature, and contain a large amount of oil. The cervical region of the vertebral column is always very short; and the seven component elements may be partially or completely fused together, while the odontoid process of the axis when present is short and blunt, and may be entirely wanting. None of the vertebræ unite to form a sacrum. The lumbar and caudal vertebræ are large and numerous, and from the absence of zygapophysial articulations allow of a large amount of motion in the hinder part of the body; the presence of chevron-bones distinguishes the caudals from the lumbars. The terminal epiphyses of the vertebræ do not unite with the centra till the animal is fully adult. The cranium presents peculiar features which it will not be necessary to describe here; although it may be mentioned that the usually small nasals are generally brought up near to the vertex, and that there is a more or less elongated rostrum in advance of the external nares, formed by the premaxilla, maxilla, mesethmoid, and vomer. Clavicles are absent; the scapula and humerus are well developed and freely movable upon one another, but the anterior bones of the limb admit of only a very slight amount of movement. There are usually five digits in the manus (fig. 1171), but these may be reduced to four; the phalangeals are unique among Mammals in exceeding the number of three to a single digit, and also in being furnished with epiphyses. The pelvis is represented by a pair of styliform bones, which are regarded as the ischia; and there are occasionally small ossifications or cartilages representing the aborted bones of the proximal part of the hind limb. Teeth are usually present, but are very variable in number and size. The dentition in existing forms is homœodont and monophyodont, but it was heterodont in the extinct *Zeuglodontidæ* of the Eocene.

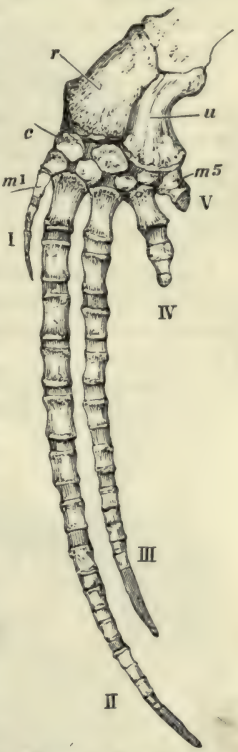


Fig. 1171.—Dorsal aspect of the left pectoral limb of the Black-fish (*Globicephalus melas*). Reduced. *r*, Radius; *u*, Ulna; *c*, Carpus (the letter placed on the scaphoid or radiale); *m*1-*m*5, Metacarpus; I.-V., Phalangeals. (After Flower.)

The Cetacea are not known with certainty before the Eocene, and are most abundant in the later Tertiary periods. The dentition of the Eocene *Zeuglodontidæ* indicates that the order has been

probably derived from Mammals with a heterodont dentition; and Professor Flower comes to the conclusion that it is most probable that their ancestors were allied to the Ungulata; while from the absence of Cetacean remains in the Cretaceous the same authority thinks that the earlier members of the order were inhabitants of freshwater. With the exception of the *Platanistidæ* and some *Delphinidæ*, all existing Cetaceans are of marine or estuarine habits.

In their increased number of phalangeals (hyperphalangism) the Cetacea resemble the Reptilian *Ichthyosauridæ* and *Plesiosauridæ*, and from this circumstance, coupled with their simple type of teeth, it has been argued that they represent the most archaic type of Mammals, and even that they are directly descended from the Ichthyosaurs. As already mentioned there are, however, many practically decisive objections to these views.

For the determination of fossil Cetaceans the solid tympanic and petrosal bones of the internal ear, and less frequently the cranial rostrum, are of especial importance, since these parts are generally well preserved.

Suborder 1. Mystacoceti.—In this suborder, commonly known as the Whalebone Whales, functional teeth are never present, although germs may be developed in the gums; "baleen" or whalebone is always attached to the palate; the tympanic bone (fig. 1172) is anchylosed to the periotic and involuted upon itself; the nasal passages are roofed in by the nasals, the lachrymal is small and distinct from the jugal; and the rami of the mandible are laterally curved, and do not meet in a symphysis.

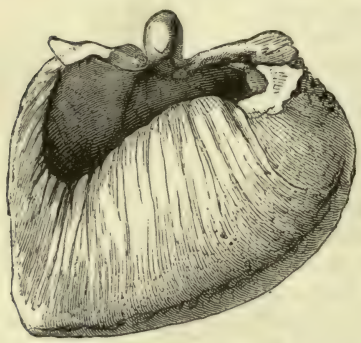


Fig. 1172.—Inner view of the right tympanic of the Greenland Whale (*Balæna mystacetus*). One-third natural size. (After Gray.)

Family Balænidæ.—The only family of this suborder may be divided into the *Balænine* and *Balænopterine* sections. In the first of these there is often no dorsal fin, the tympanic (fig. 1172) has a characteristic flattened and angulated shape, and some or all of the cervical vertebræ are at least usually fused together. Remains of the genus *Balæna* (including *Balænotus* and *Balænula*) occur abundantly in the Pliocene, and especially in the English and Belgian Crags. One of these fossil species (*B. affinis*) is closely allied to the Greenland Whale (fig. 1173); while *B. primigenia* is more nearly related to

the Right Whales of the Southern Seas. *Palæocetus*, which has been regarded by its describer as of Mesozoic age, may be provisionally referred to this section; the type was probably obtained from the Red Crag. In the *Balænopterine* section a dorsal fin is very generally present (whence the name "Finners" applied to many of these

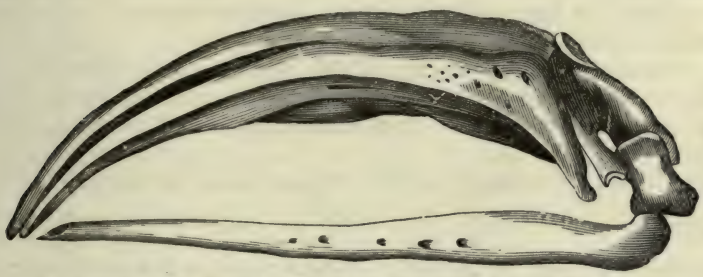


Fig. 1173.—Left lateral view of the skull of the Greenland Whale (*Balæna mystacetus*). Greatly reduced. (After Owen.)

Whales); the cervical vertebræ are free, and thicker than in the *Balænine* section; and the tympanic (fig. 1174) is longer, more inflated, and more rounded than in the latter. The existing genus *Megaptera* (in which may be included the fossil *Burtinopsis*) is abundantly represented in the Pliocene Crags of both England and Belgium. *Balænoptera* also occurs commonly in the same deposits; *B. definita* being apparently nearly allied to the existing *B. sibbaldi*,

Fig. 1174.—Inner view of the right tympanic of a Rorqual (*Balænoptera musculus*). Recent. One-half natural size. (After Gray.)

which attains a length of 80 feet; while *B. emarginata* comes nearer to the living *B. rostrata*, which is seldom more than 30 feet in length, *Cetotherium* (including *Cetotheriophanes*, *Plesiocetus*, and *Plesiocetopsis*) is characterised by the narrowing of the anterior extremity of the tympanic, and is likewise found in the Crags and other Pliocene

beds; while *Herpetocetus* from the same deposits is an allied genus with an egg-shaped tympanic, and a talon to the mandibular condyle, which recalls that of *Physeter*. The names *Amphicetus*, *Idiocetus*, *Isocetus*, *Heterocetus*, and *Mesocetus*, have been applied to Cetaceans from the Belgian Crag, most or all which may apparently be included in *Cetotherium*. Lastly, a vertebra from the Upper Eocene of Hampshire has been referred to *Balænoptera*, but this reference requires confirmation.

Suborder 2. Archæoceti.—This suborder is confined to the Eocene and Lower Miocene, and may be characterised by the long nasals, and the presence of teeth differentiated into groups in both jaws.

Family Zeuglodontidæ.—In the one genus of the only known family the dental formula is $I.\ \frac{3}{3},\ C.\ \frac{1}{1},\ Pm.+M.\ \frac{5}{5}$. The cutting-teeth are simple and pointed; but the cheek-teeth (fig. 1175)

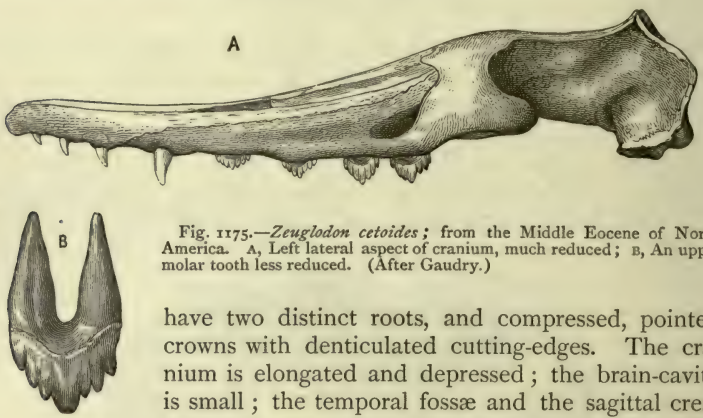


Fig. 1175.—*Zeuglodon cetoides*; from the Middle Eocene of North America. A, Left lateral aspect of cranium, much reduced; B, An upper molar tooth less reduced. (After Gaudry.)

have two distinct roots, and compressed, pointed crowns with denticulated cutting-edges. The cranium is elongated and depressed; the brain-cavity is small; the temporal fossæ and the sagittal crest are large; the cranial rostrum is long, and on the sides largely composed of the premaxillæ; the nasals are long, flat, and narrow; and the external nares are placed more anteriorly than in living Cetaceans. All the cervical vertebræ are free, while those of the lumbar region are unusually elongated; but the nature of the limbs is not known. In their dentition, as well as in the characters of the skull—especially the long nasals and the forward position of the nares—the Zeuglodonts depart less markedly from the general plan of Mammalian structure than any existing members of the order; and it is remarkable that the Mystacoceti show a nearer resemblance in cranial structure to these fossils than is made by the Odontoceti. The one genus *Zeuglodon* is known from the lower Tertiaries of Egypt, England, and North America; the remains of

the typical *Z. cetoides* being extraordinarily abundant in parts of the latter country, where they have been weathered out of a deposit of Middle Eocene age.

Suborder 3. Odontoceti.—All living Cetaceans not included in the Mystacoceti belong to this suborder, which is characterised by the presence of calcified teeth after birth; the functional ones being generally numerous, but sometimes reduced to a single pair (occasionally wanting). Baleen, or whalebone, is invariably absent; the cranium is more or less unsymmetrical; the nasals are reduced to mere bony nodules which do not roof over the narial passages; the lachrymal is either united to the jugal, or of very large size; and the mandibular rami are nearly straight, and meet in a median symphysis. The tympanic is not anchylosed to the periotic, and has not the completely involuted structure found in the Mystacoceti.

Family Physeteridæ.—In this family there are no functional teeth in the upper jaw; and the anterior facet of the periotic for articulation with the tympanic is smooth (fig. 1176), while the posterior tympanic surface of the former bone is broad, with a distinct median ridge. In recent genera some or all of the cervical vertebræ are fused together. This family is divided into the two subfamilies *Physeterinæ* and *Ziphiinæ*. In the former, which comprises the existing Cachalot, or Sperm Whale (*Physeter*), and the Short-nosed Cachalot (*Cogia*), the mandibular teeth are numerous and implanted in a long groove partly divided by imperfect septa. Remains of the gigantic Sperm Whale (*P. macrocephalus*) are found in the English Forest-bed, and also in the Pleistocene of South America; the large teeth have no enamel at their summit. Allied to this genus are *Eucetus* from the English and Belgian Crags, and *Physetodon* from the Pliocene of Australia; while *Physeterula* is a genus founded on a whale from the former deposits, which does not exceed some 20 feet in length. A number of Pliocene and Miocene forms apparently allied to the Cachalot, but with the crowns of the teeth tipped with enamel, have been described as *Balænodon*, *Scaldicetus*, *Hoplocetus*, *Physodon*, and *Ziphioides*; *Hoplocetus* and *Physodon* comprise comparatively small species from the English and Belgian Crags and the French Miocene; while *Ziphioides* is from the Middle Miocene of Baltringen in Würtemberg. In the Ziphiine subfamily, comprising the existing Bottle-nosed (*Hyperöodon*) and Beaked-Whales (*Ziphius* and *Mesoplodon*), all the mandibular teeth, with the exception of one or

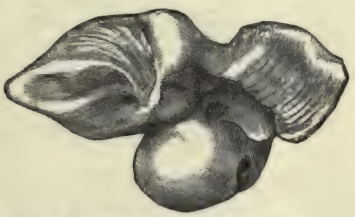


Fig. 1176.—The left periotic of *Mesoplodon longirostris*; from the Suffolk Crag.

occasionally two pairs, are rudimentary. *Hyperöodon* is represented in the Crags of England and Belgium. These beds also yield the extinct genus *Choneziphius*, as well as several species belonging to the living genus *Mesoplodon*, which is distinguished from *Choneziphius* by the complete ossification in the adult of all the elements comprising the cranial rostrum. The Crag species of *Mesoplodon* are mainly known by these solid rostra, which in the living species are composed of dense ivory-like bone, and are the most solid bones found in the whole of the Vertebrata. The periotics (fig. 1176) are more rarely found, but are equally characteristic.

Family Platanistidæ.—This family, which is now represented by *Platanista* of the Ganges, and *Inia* and *Pontoporia* of the great rivers of South America, is characterised by the large number of simple teeth in the elongated jaws, and by the length of the mandibular symphysis exceeding half that of the entire mandible. None of the cervical vertebræ are anchylosed together. Remains allied to *Pontoporia* were found by Bravard in the Pleistocene of South America, but these are referred by some authorities to a distinct genus under the name of *Pontistes* or *Palæopontoporia*. The extinct genera *Champsodelphis* and *Schizodelphis*, of the European Pliocene, are usually referred to this family, but the latter approximates to the *Delphinidæ*.

Family Squalodontidæ. — The extinct Squalodonts were formerly classed with the *Zeuglodontidæ*, but the characters of the cranium are essentially Delphinoid, although the teeth are differenti-

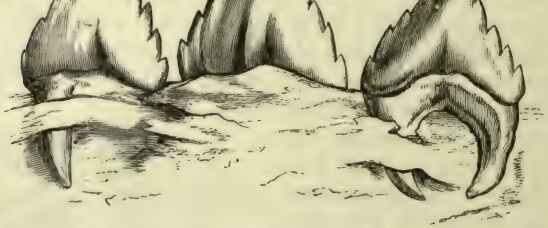


Fig. 1177.—Three lower molars of *Squalodon*; from the Miocene of Europe.

ated into groups as in the former. The type genus *Squalodon* ranges from the Middle Miocene to the Pleistocene of Europe, and is also found in the Tertiaries of North America, New Zealand, and Australia. The teeth may be arranged as $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{4}{4}$, $M.\frac{7}{7}$; the premolars are simple, but the true molars (fig. 1177) have double roots, and crowns very like those of *Zeuglodon*, although

distinguished by the denticulations being more developed on the posterior than on the anterior border. The so-called *Rhizoprion* is merely a species of this genus.

Family Delphinidæ.—In this, the last family of the Cetacea, the teeth are simple, and usually numerous in both jaws; and the length of the mandibular symphysis may be very small, and never exceeds one-third of that of the entire ramus. The periotics (fig. 1179), which are frequently found in a fossil condition, are readily distinguished from those of the *Physeteridæ*, by having the anterior facet which articulates with the tympanic marked by a

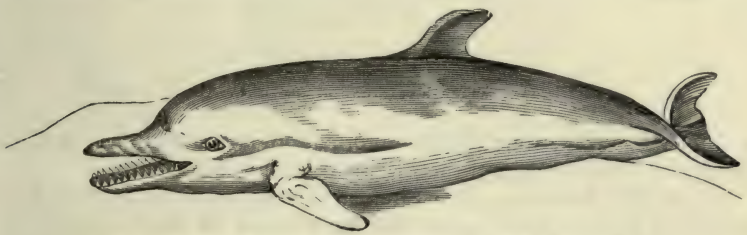


Fig. 1178.—The common Dolphin (*Delphinus delphis*). Reduced.

number of grooves, as well as by the narrowness of the posterior half of their tympanic aspect. This family comprises all the Cetaceans commonly known as Porpoises, Grampuses, Killers, and Dolphins. Remains of the Narwhal (*Monodon monoceros*) are found in the Norfolk Forest-bed and the Pleistocene of Alaska. The genus *Delphinapterus*, now represented by the "White Whale," occurs in the Lower Pliocene of Tuscany, as well as in the Pliocene and Miocene of other parts of Europe. An extinct species of "Killer-Whale" (*Orca*) is found in both the Italian and English Pliocene. The existing *Globicephalus melas*, or "Black-fish," has left its remains in the superficial deposits of Essex; while the extinct *G. uncidens* occurs in the Suffolk Crags. A left periotic of the latter species is represented in fig. 1179, in order to show the features characteristic of this family. The existing *Pseudorca crassidens* was originally described from a subfossil cranium found in the fens of Lincolnshire. Of the smaller Dolphins it is probable that the genera *Tursiops*, *Lagenorhynchus*, and *Delphinus* (as now restricted) are all represented in the Pliocene of Europe. *Eurhinodelphis* is a long-snouted genus from the Pliocene of Belgium and Italy, which is

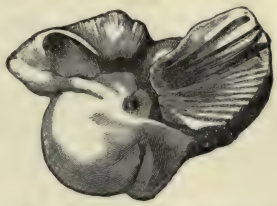


Fig. 1179.—The left periotic of *Globicephalus uncidens;* from the Coralline Crag of Suffolk.

probably nearly related to the existing *Steno*. Delphinoid remains from the Miocene of North America have been described by Professors Leidy and Cope under the names of *Priscodelphinus*, *Tetrosphys*, *Zarhachis*, *Lophocetus*, *Rhabdosteus*, *Ixacanthus*, *Anoplonassa*,

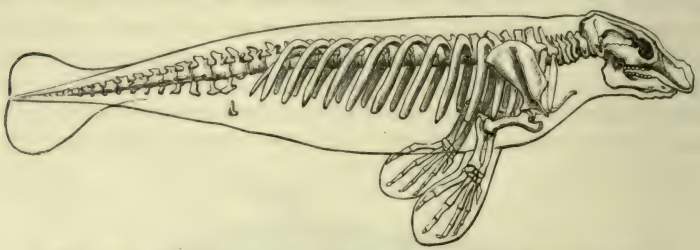


Fig. 1180.—Skeleton of the Manatee (*Manatus australis*). Greatly reduced.

and *Orycterocetus;* but further information is required as to the affinity of these forms and their right to generic distinction.

Order V. Sirenia.—The Sirenia, now represented only by the Manatees and Dugongs, agree with the Cetacea in their adaptation for a purely aquatic life, and accordingly present a strong general resemblance in their external contour to the members of that order. The head is, however, of normal relative size; the tail has a hori-

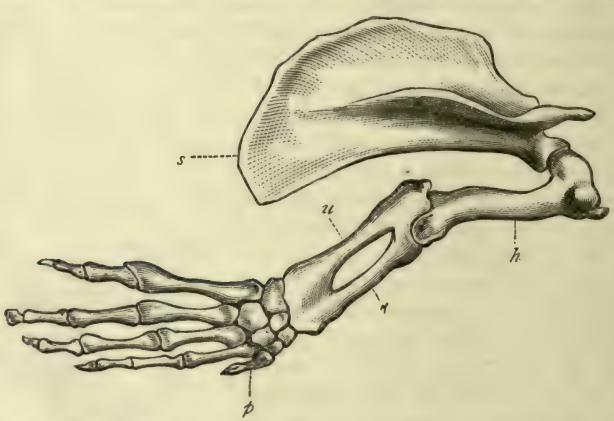


Fig. 1181.—Dorsal view of the right pectoral limb of *Manatus australis*. Much reduced. *s*, Scapula; *h*, Humerus; *r*, Radius; *u*, Ulna; *p*, Pollex.

zontal membranous expansion; the pectoral limbs, although modified into paddles (fig. 1181), retain the normal number of phalangeals; all external traces of the pelvic limbs are wanting; and the surface of the body is either naked or covered with sparse bristles. The lips are fleshy; the nostrils placed near the extremity of the muzzle

(fig. 1180); the eyes minute; and the small ear has no external pinna. The bones of the skeleton are extremely dense and solid; the cervical vertebræ may be reduced to six, but are never anchylosed together; and the axis has a well-developed odontoid process. The vertebræ have no epiphyses; and none of them unite to form a sacrum. Large chevron-bones are present. Clavicles are wanting; and no recent forms show any trace of the femur, although a styliform rudiment of this bone is found in the extinct *Halitherium*. The two bones of the forearm in the existing genera (fig. 1181) are subequal in size, and frequently anchylosed together. In recent forms the skull (fig. 1182) is remarkable for the upward direction

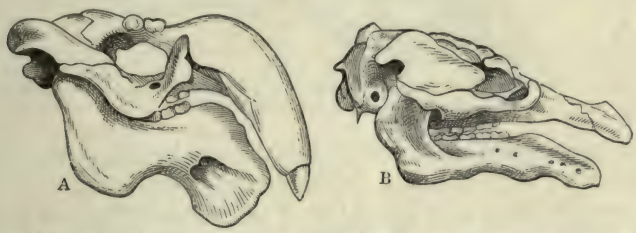


Fig. 1182.—Right lateral view of the skulls of *Halicore* (A) and *Manatus* (B). Much reduced.

of the narial aperture, and for the absence or rudimental condition of the nasals. The teeth can only be differentiated in the living genera into incisors and cheek-teeth, which are separated from one another by a long interval; but in one fossil genus there is a more complete dental series; while in *Rhytina* these organs were totally wanting. In the existing genera the dentition is monophyodont, but milk-molars occur in *Halitherium*. This order is known from the Eocene upwards, but appears to have been steadily dying out to the present period. The fossil forms, although decidedly more generalised than their living representatives, do not at present afford any clear indication as to the origin of the order.

Family Halicoridæ.—In this family the one existing genus *Halicore* (Dugongs) has the deflected premaxillæ (fig. 1182, A) furnished with a pair of large tusk-like incisors; and there are also four pairs of functionless germs of cutting-teeth in the similarly deflected mandibular symphysis. Five or six cheek-teeth are developed in each jaw, which are usually cylindrical, and all grow from persistent pulps, and are not coated with enamel. The Dugongs inhabit the coasts of the Red Sea and the Indian Ocean. *Prohalicore*, from the Pliocene of France, is regarded as nearly allied to the existing genus. The only other form which has been referred to this family is known by a molar from the Tertiary of California, which has been described by Professor Marsh under the name of

Desmotylus. Further information is, however, required before this reference can be definitely accepted.

Family Halitheriidæ.—The fossil forms constituting the *Halitheriidæ* are characterised by the presence of upper incisors; by the cheek-teeth being coated with enamel, like those of the *Manatidæ;* and by the retention, in at least some cases, of a milk dentition.

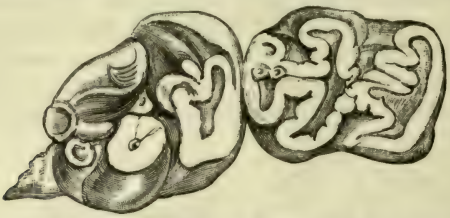


Fig. 1183.—Grinding surface of the penultimate and last right lower molars of *Halitherium fossile;* from the European Miocene.

In the type genus *Halitherium* (which may be taken to include *Halianassa*, *Pugmeodon*, and *Felsinotherium*) there is a pair of tusk-like upper incisors, and either five or six cheek-teeth in each jaw; small nasals are present in at least some of the species; the premaxillæ and mandibular symphysis are bent downwards; there is a descending plate at the angle of the mandible; and a small rod-like ossification represents the femur. The molars (fig. 1183) have a pattern on their grinding surface resembling that of *Hippopotamus*.

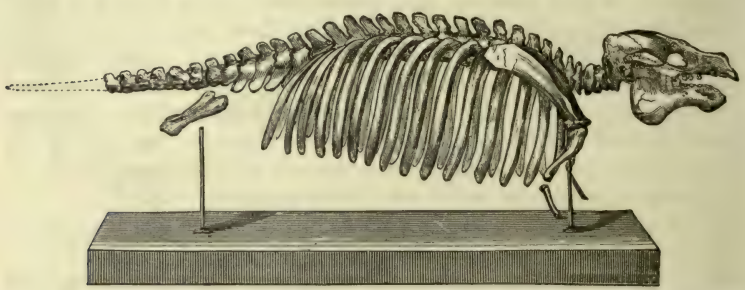


Fig. 1184.—Skeleton of *Halitherium Schinzi;* from the Lower Miocene of Hessen-Darmstadt. Much reduced.[1]

This genus ranges from the Lower Miocene (Middle Oligocene) to the Lower Pliocene of Europe; and remains of *H. Schinzi* (fig. 1184) are especially abundant in the Lower Miocene sands of certain districts of Hessen-Darmstadt. *Prorastomus*, from Tertiary strata in the West Indies, is a generalised form apparently

[1] In this figure the deflection of the premaxillæ is omitted.

allied to *Halitherium*, but with a fuller dentition, and without the marked deflection of the extremities of the jaws. The dentition is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.+M.\frac{7 \text{ or } 8}{7 \text{ or } 8}$; the upper incisors are not tusk-like; and the cheek-teeth have simple transverse ridges somewhat like those of the Ungulate genera *Dinotherium* and *Listriodon*. *Eotherium* is definitely known by a cast of the brain-cavity from the Eocene of Egypt, but teeth from the same deposits described under the name of *Manatus* may perhaps belong to it; its affinities cannot yet be properly determined. Probably allied to *Halitherium* is *Crassitherium* from the Pliocene of Belgium; while *Dioplotherium* from the Miocene of South Carolina is regarded as intermediate between *Halicore* and *Halitherium*.

Family Rhytinidæ.—The *Rhytinidæ* are known only by the huge *Rhytina gigas*, or Steller's Sea-Cow, which was formerly very abundant on Behring and Copper Islands in the North Pacific, but is commonly supposed to have been exterminated about 1768, although a few individuals may have lingered on to a considerably later date. The Rhytina attained a length of from 20 to 25 feet, and is characterised by the entire absence of teeth, their function being supplied by horny plates (cornules) on the palate. The head is very small in proportion to the length of the body; and has the premaxillæ and mandibular symphysis moderately deflected. The skin was naked, and covered with a rugged epidermis resembling the bark of a tree. Nearly entire skeletons have been obtained from the peat of Behring Island.

Family Manatidæ.—In *Manatus*, the only known representative of this family, the premaxillæ and mandibular symphysis (fig. 1182, B) are not deflected, and there are no functional incisors. The cervical vertebræ are reduced to six; the cheek-teeth, which are coated with enamel and carry two transverse ridges, may be as many as eleven in each jaw, although it is seldom that more than six are present at any one time. The Manatees are inhabitants of the mouths and estuaries of the great rivers discharging into the two sides of the Atlantic. No fossil forms are known which can be referred with certainty to this family, although the type generic name has been applied to certain teeth from the Eocene of Egypt already mentioned.

As Sirenians of uncertain affinity may be mentioned *Chronozoum* from the later Tertiary of New South Wales; *Hemicaulodon* from the Eocene of Shark River; *Pachyacanthus* from the Miocene of Vienna; and *Trachytherium* (with which *Rhytiodus* may perhaps be identical) from that of France.

CHAPTER LXI.

CLASS MAMMALIA—continued.

Order Ungulata.

Order VI. Ungulata.—The Ungulata, or Hoofed Mammals, constitute the largest and one of the most important orders into which the class is divided; all the included groups being so connected together as to preclude their division into well-defined separate orders. This order comprises at least seven suborders, of which three are totally extinct, while all the others, with the exception of the Hyracoidea, have lost a large number of family types at the present day. The two first suborders—Artiodactyla and Perissodactyla—present several features in common, and are accordingly brigaded together by some authorities under the names of Ungulata Vera, Clinodactyla, or Diplarthra; while all the others are included in a second division under the name of Subungulata.

All the members of this order are adapted for a terrestrial life, and in the main for a vegetable diet, although a few are more or less omnivorous. Their dentition is heterodont and diphyodont, and the milk-set is well developed, and not changed till late in life; and in the Perissodactyla alone among Mammals do we find certain instances where the whole four premolars are preceded by milk-teeth. The cheek-teeth of the more typical forms have broad crowns, with either tuberculated or ridged surfaces; and their crowns are very frequently interpenetrated by deep folds of enamel, which produce a complicated pattern on their worn surfaces. Except in *Typotherium*, clavicles are always wanting. The toes, with the exception of *Chalicotherium*, are provided either with blunt, broad nails, or with hoofs more or less completely encasing the terminal phalangeals. The feet of existing types are digitigrade, and the number of the toes varies from five to one. In all existing forms the humerus has no entepicondylar foramen. The scaphoid and

lunar bones of the carpus are always distinct; but the radius and ulna may unite.

In the great majority of instances the cheek-teeth are rooted, and in the suborders Artiodactyla, Perissodactyla, and Proboscidea, which comprise the most specialised members of the order, a gradual increase in the height of the crowns of these teeth may be traced from the generalised to the specialised genera. Those teeth in which the crowns are low, and their whole structure is visible from the grinding surface, being known as *brachydont* (compare fig. 1195); while those with high crowns, in which the bases of the enamel-folds are invisible from the grinding surface, are termed *hypsodont* (fig. 1220). The change from a brachydont to a hypsodont dentition is accompanied by the production of a nearly flat and horizontal grinding surface in the cheek-teeth, in place of a more or less strongly ridged one; the more specialised type being adapted for a perfect grinding action of the upper against the lower teeth, while in the more generalised type the action is to a great extent a snapping one. Examples of the former type are shown by the Horse and Ox, and of the latter by the Pig and Hyrax. Hypsodontism is not confined to this order, as will be noticed in the sequel.

Some remarks on the probable origin of the order are made below under the head of the Condylarthra. In the specialised forms there is very often a tendency to a suppression of the anterior teeth, more especially in the lower jaw.

Suborder 1. Artiodactyla. — This and the next suborder present certain structural modifications of the extremities, by which they are distinguished from the remaining five suborders, and on which account, as already mentioned, they are grouped together by some writers under the name of Ungulata Vera, or Diplarthra. Thus the feet are never plantigrade, and the number of functional digits does not exceed four. In the carpus (fig. 1185) the scaphoid is supported by and largely articulates with the magnum; while the latter (together with the unciform) supports the lunar, and has no connection with the cuneiform. In the tarsus the cuboid extends inwardly to articulate with the astragalus, which is deeply grooved (fig. 1186). All the component bones of both the carpus and tarsus strongly interlock, which makes the structure of these joints more complex than in the other suborders. Finally, the jugal forms the anterior part of the zygomatic arch (fig. 1187), and the brain is of relatively large size and complex structure.

This suborder, so far as at present known, is distinguished from the Perissodactyla by the distal surface of the astragalus (fig. 1186) being ginglymoid, by the third and fourth digits (fig. 1185) being equal in size, and arranged symmetrically on either side of a line drawn between them; by the absence of a third trochanter

to the femur; and by the articulation of the fibula with the calcaneum. In all existing forms the number of the dorso-lumbar

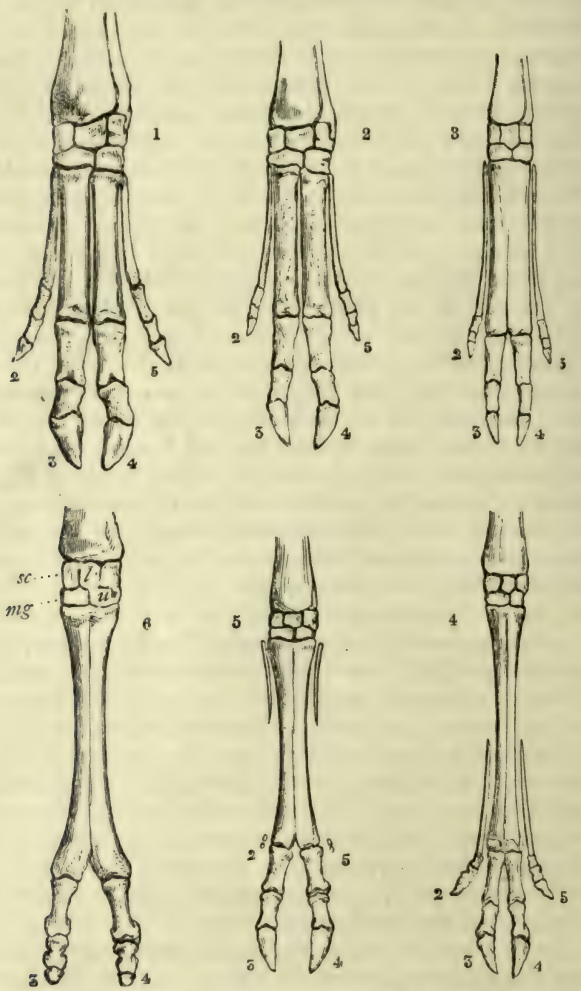


Fig. 1185.—Left manus of (1) Pig (*Sus*), (2) *Hyomoschus*, (3) Chevrotain (*Tragulus*), (4) Roebuck (*Capreolus*), (5) Sheep (*Ovis*), and (6) Camel (*Camelus*). In the carpus the middle bone in the upper row is the lunar, the left the scaphoid, and the right the cuneiform; in the second row the left bone is the magnum, and the right the unciform. Reduced. (After Dawkins and Oakley.)

vertebræ is nineteen; and the nasals are not expanded posteriorly. In the dentition the first tooth of the cheek series never has a deciduous predecessor. The upper premolars are very generally

more simple in structure than the true molars; while the last lower true molar nearly always has a third lobe, the same feature being repeated in the last lower tooth of the milk series.

In the Pecora the pelvis (fig. 1128 *bis*) is characterised by the great length of the ilia, which are not much expanded; but in the Hippopotamus these bones are shorter and more expanded, and thus approximate to those of the Perissodactyla. The symphysis of the ischia and pubes is much elongated. The true molars in the upper jaw carry either four or five main columns; in the less specialised forms such as the Pigs (figs. 1194, 1195), such columns in both upper and lower molars form low subconical tubercles, when the dentition is termed *bunodont;* but in others, such as *Eporeodon* (fig. 1201) and the Ruminants (fig. 1220), the outer pair of columns becomes transversely flattened, and the inner pair crescent-shaped, and the dentition is then termed *selenodont.* In the lower molars of the latter type of dentition it is the inner columns that become flattened, while the outer ones assume a crescent shape. There is, however, a complete passage from the one type to the other; the most specialised forms with a hypso-selenodont dentition being of comparatively recent origin. The existing members of this suborder are divided into the sections Suina (Pigs and Hippopotamus), Tylopoda (Camels), Tragulina (Chevrotains), and Pecora (typical Ruminants); but since such divisions will not hold good for the fossil forms, it will be convenient merely to divide the suborder into families.

Fig. 1186.—Left astragalus of a Ruminant Artiodactyle (*Bos*). Reduced.

It should, moreover, be observed that it is by no means certain that all the above-mentioned characters will apply to some of the less known earlier members of the suborder, since some of these included in the *Anoplotheriidæ* present certain remote indications of affinity with the Perissodactyla.

The advance from a bunodont to a hypso-selenodont dentition is accompanied in this suborder by a tendency in the second and third metapodials to coalesce into a *cannon-bone*, and also by a change in the form of the odontoid process of the axis vertebra from a peg-like projection to a spout-like demicylinder. The earliest form which has been referred to this suborder is the small *Pantolestes*, from the Lower Eocene of the United States. This genus is still very imper-

fectly known; but Professor Cope, who makes it the type of a distinct family, states that it has tritubercular upper molars, and four digits in the pes, and looks upon it as the ancestral type of the Camels. Dr Schlosser is, however, not satisfied that the teeth are

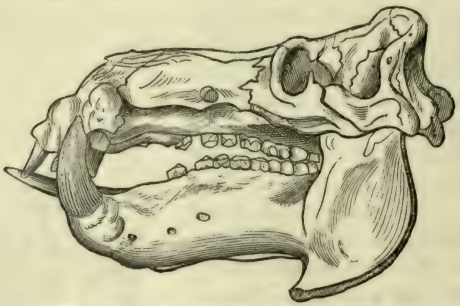


Fig. 1187.—Left aspect of the Hippopotamus (*H. amphibius*). Much reduced. (After Giebel.)

really tritubercular, and suggests that it may indicate a transitional type between the Artiodactyla and the Condylarthra.

Family Hippopotamidæ.—This family contains the single Old World genus *Hippopotamus*, now represented by two species of

Fig. 1188.—Left manus of *Hippopotamus amphibius*. Reduced. (After Cuvier.)

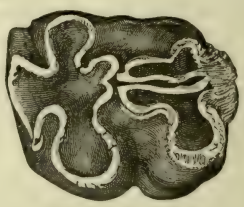


Fig. 1189.—Left upper true molar of *Hippopotamus amphibius*. Two-thirds natural size.

bulky animals, which spend a large proportion of their time in the waters of lakes and rivers. In the skull (fig. 1187) the angle of the mandible has a descending flange; the facial portion is much elon-

gated; and the orbits are tubular and very prominent. The dental formula is $I.\ \frac{(2-3)}{(1-3)}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{4}{4}$, $M.\ \frac{3}{3}$. The cheek-teeth are bunodont in structure; the true molars (fig. 1189) having four columns, which present trefoil-shaped dentine surfaces when worn; the premolars are simpler. The upper incisors are short and vertical (fig. 1187), but those of the lower jaw are procumbent, and may be very large (fig. 1191). The canines of the upper jaw are curved upwards like those of pigs, while the lower ones are of enormous size, and have their extremities obliquely worn to a cutting-

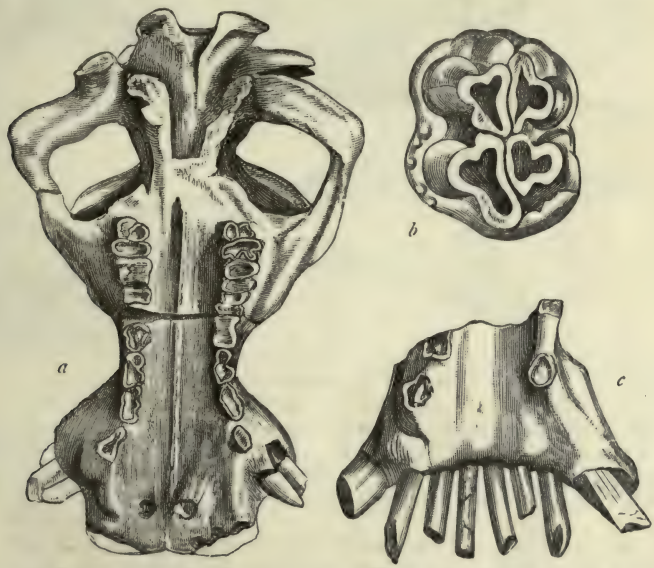


Fig. 1190. —*Hippopotamus sivalensis;* from the Pliocene of the Siwalik hills. *a*, Palatal view of cranium; *b*, Third right upper true molar; *c*, Symphysis of mandible. Reduced.

edge by biting against the outer surfaces of those of the upper jaw. The feet (fig. 1188) are short and massive, and furnished with four digits, of which the terminal phalangeals bear nail-like hoofs. The skin is nearly naked and of great thickness; while the ears and eyes are very small, and the tail is short.

In the more generalised forms like *H. sivalensis* (fig. 1190), of the Pliocene of the Siwalik Hills of India, there are three pairs of incisors in both jaws, all of which are of subequal size. This hexaprotodont group is represented in the Pliocene of Burma by *H. iravaticus*, and in that of Algiers by *H. bonariensis;* while its latest member is *H. namadicus*, of the Pleistocene of the Narbada Valley, in India. In the latter deposits

also occurs *H. palæindicus*, in which the second lower incisor is very minute, and perhaps disappears in the adult; while in the existing *H. amphibius* of Africa, which is found fossil in Europe from the Upper Pliocene of the Val d'Arno to the late Pleistocene, there are only two pairs of incisors in each jaw, the innermost pair in the mandible being of enormous dimensions (fig. 1191). It is evident from the condition prevailing in *H. palæindicus* that it is the second pair of incisors which is missing in the existing species. Allied to, but smaller than the latter, are *H. Pentlandi* and *H. minutus*, whose remains are found in enormous quantities in the caves of Italy and the Mediterranean islands. Finally,

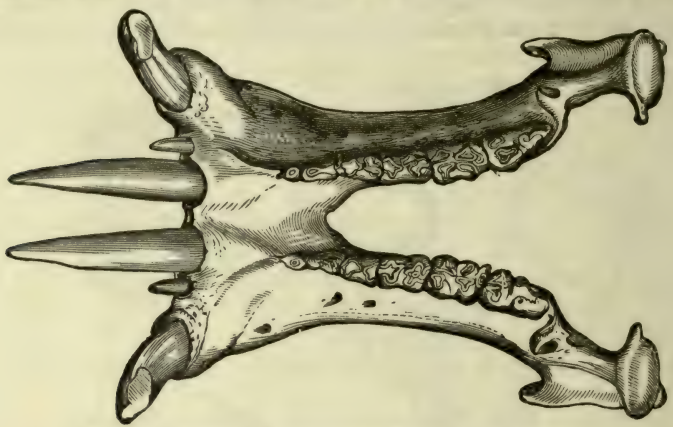


Fig. 1191.—Mandible of *Hippopotamus amphibius*. Reduced.

in the small *H. liberiensis*, now living in West Africa, the number of lower incisors is reduced to a single pair. The resemblance of the mandible of *Hippopotamus* to that of the *Anthracotheriidæ* suggests that both are derived from a common ancestor.

Family Suidæ.—This family may be taken to include both the existing *Dicotylidæ* and *Phacochœridæ* and the extinct *Listriodontidæ*, since fossil forms indicate a close connection between all these types. The cheek-teeth are typically bunodont and brachydont, the upper true molars carrying four main columns, which may be either simple (fig. 1195) or of extreme complexity (*Hippohyus*), but which do not wear into distinct trefoils. Their outer and inner columns may, however, coalesce into transverse ridges (fig. 1193). The skull (fig. 1192) has a more or less elevated supraoccipital region, from which the profile slopes away to the muzzle, the nasals being frequently much elongated; while the mandible has no descending flange at the angle. The canines are frequently large and tusk-like (fig. 1192), the superior ones being curved upwards, and the lower ones biting against a facet on the outer surface of the upper ones; but in many of the earlier forms, and in the recent Peccaries, the

development of these teeth is much less marked. The digits are usually four in number, but in the existing forms (fig. 1185) only

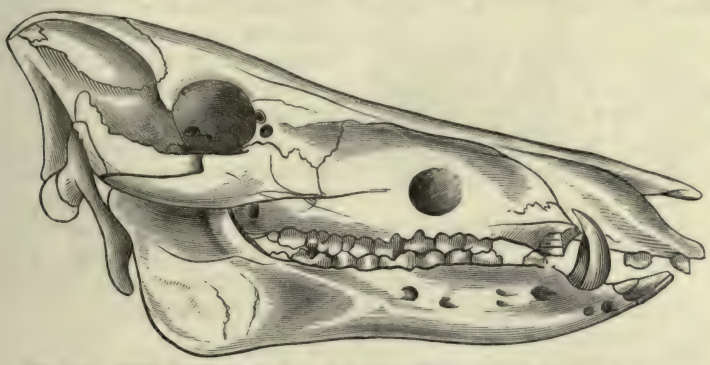


Fig. 1192.—Right lateral aspect of the skull of the Wild-boar (*Sus scrofa*). Reduced. (After Gray.)

the two middle ones touch the ground. The dental formula is very generally the typical one.

The extinct genus *Listriodon* differs from all the other members of the family in that the true molars (fig. 1193) carry a pair of simple transverse ridges. The dental formula is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{3}{3}$, $M.\frac{3}{3}$; the canines form large tusks; the last upper premolar is simpler than the true molars; and the anterior premolars are relatively wide. The skull is essentially that of a Pig. Remains of *Listriodon* occur in the Middle Miocene of the Continent (where they have been described under the names of *Lophiochœrus* and *Tapirotherium*), and also in the Pliocene Siwaliks of the Punjab and Sind. The molars present the same relation to those of *Sus* as is borne by the molars of *Dinotherium* to those of many species of *Mastodon*.

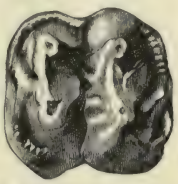


Fig. 1193.—The second left upper true molar of *Listriodon splendens*; from the Middle Miocene of France.

Leaving this aberrant type, we may turn to the typical genus *Sus*, in which the normal dental formula is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{4}{4}$, $M.\frac{3}{3}$, although the first premolar is absent in some fossil species, and also in the African *Potamochœrus*, which cannot be palæontologically separated. The canines are developed into tusks (fig. 1192), although they are small in the earlier species. The crowns of the upper true molars are oblong, and both the upper and lower last true molars (fig. 1194) have a third lobe, although its degree

of development varies greatly; and these teeth do not come into use until the first molar has been well worn. The anterior premolars are compressed, and there is no diastema between the first and the second. The upper premolars are simpler than the true molars, and there is considerable difference in the number of accessory tubercles developed in the latter; those species in which these are most numerous showing a more complex pattern on the worn crowns. The molars of some of the earlier forms approximate to those of *Hyotherium*.

Fig. 1194.—The third right lower true molar of *Sus cristatus*; India. *a*, *d*, Middle columns of talon.

The species with the most complicated molar structure are *S. Falconeri* of the Pliocene of the Siwalik Hills, *S. phacochœroides* of the Pliocene of Algeria, *S. karnuliensis* of the Pleistocene caves of Madras, and the living Indian *S. cristatus* (fig. 1194), which is also found fossil in the same caves; the last lower true molar of the first-named species making a decided approach to that of *Phacochœrus*. In the European Wild-boar, which is found fossil as low down as the Norfolk Forest-bed, the hind lobe of the last molar is of moderate complexity. *S. titan*, and *S. giganteus* of the Siwalik Hills of India, together with *S. antiquus*, *S. erymanthius*, and *S. major* of the Lower Pliocene of Europe, are large species with comparatively simple molars; the first being the largest known species, and fully equal in size to a Tapir. *S. hysudricus* of the Siwalik Hills, *S. palæochœrus* of the Lower Pliocene of Eppelsheim, and *S. chœroides*, which has been recorded from France and the Middle Miocene of Tuscany, are small species with simple molars like those of the living *S. andamanensis*, to which they may be allied. *S. arvernensis* of the Upper Pliocene of France is closely related to the living African *S.* (*Potamochœrus*) *africanus*; while in the small *S. punjabiensis* of the Pliocene of north-western India we probably have the direct ancestor of the Pigmy-hog (*S. salvanius*) of the terai-lands of Nipal. No representatives of the genus occur in America; and *S. chœroides* seems to be the earliest species.

Here it will be convenient to notice the African Wart-hogs (*Phacochœrus*) which appear to be related to some of the specialised fossil species of *Sus*. The dental formula is $I.\ \frac{1}{(2-3)}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{2}{3}$, $M.\ \frac{3}{3}$, but the whole of the teeth with the exception of the canines and the last true molars may be lost in the adult, thus presenting a very remarkable instance of extreme specialisation. The last true molar is a very peculiar tooth, consisting of a great number of tall agglomerated columns, or denticules; but a marked approach to this structure is presented in some of the species of *Sus* from the

Pliocene of Algeria and India. Remains of *Phacochœrus* occur in superficial deposits in Africa. The last molar of this genus compared with that of *Hyotherium* presents a difference analogous to that between the corresponding teeth of *Mastodon* and the Mammoth.

We may now revert to the consideration of more generalised types. The most important is *Hyotherium* (in which may be included *Palæochœrus* and *Chœromorus*) which presents characters connecting it with *Dicotyles*, *Sus*, and *Chœropotamus*, and may have been the ancestor of the first two of these genera. The upper true molars (fig. 1195) have low, square crowns, with a rudimentary fifth column, which is fully developed in *Chœropotamus;* and the last true molar comes into use before the first is worn. In the third upper true molar there is no third lobe, and this lobe is small in the corresponding lower tooth; while occasionally the last upper premolar has only a single outer column, as in *Chœropotamus*. The canines are scarcely larger than the incisors; are oval in section, and the lower one is not received into a notch in the upper jaw. The lateral metapodials are stouter than in modern pigs. In Europe this genus ranges from the Quercy Phosphorites to the Middle Miocene of the Continent; while in India it occurs in the Lower Siwaliks of Sind, and also in Perim Island (fig. 1195); the American forms which have been referred to this genus are regarded by Professor Cope as distinct. *Hippohyus*, of the Indian Siwaliks, appears to be an allied but specialised form, in which the crowns of the molars are much taller, and have lateral infoldings of the enamel, whereby an extremely complex pattern is produced on their worn surfaces. *Sanitherium* of the Siwaliks must be placed with this group; while *Doliochœrus* of the Quercy Phosphorites is apparently allied to *Hyotherium*, although it may also have affinity with *Cebochœrus*. The genus *Babirusa*, of Celebes, is unknown in a fossil state.

m. 1. *m.* 2. *m.* 3.

Fig. 1195.—The left upper true molars of *Hyotherium perimense;* from the Pliocene of India.

In the John Day Miocene of the United States there occur pig-like animals apparently connecting *Hyotherium* with the existing Peccaries, most of which may be included in the genus *Chœnohyus*. These forms agree with *Hyotherium* in having the fourth upper premolar simpler than the true molars, but have the lower canine with

a triangular section, and received into a notch in the upper jaw, as in the Peccaries. The typical forms have only three premolars, but in others, which it has been proposed to separate generically as *Bothrolabis*, there are four of these teeth. Allied, or probably identical forms have been described as *Thinohyus* and *Perchœrus*, the former having four premolars. The existing South American genus *Dicotyles* includes the well-known Peccaries, and has the dental formula $I.\frac{2}{3}$, $C.\frac{1}{1}$, $Pm.\frac{3}{3}$, $M.\frac{3}{3}$. The structure of the small canines has been already mentioned; the last upper premolar has four columns like the true molars (fig. 1196); while the third upper

Fig. 1196.—Grinding surface of the right upper cheek-teeth of a Peccary (*Dicotyles labiatus*). (After Giebel.)

true molar, which comes into use before the first is worn, has no distinct third lobe. In the pes the phalangeals of the fifth digit are aborted. Remains of two existing and one much larger extinct species of this specialised genus are found in the Pleistocene deposits of the Brazilian caves; while large Peccaries also occur in the Pliocene of the United States and the Pleistocene of Mexico, which have been described as *Platygonus*, but may be included in the type genus, although they have rather simpler premolars.

Family Chœropotamidæ.—The true molars of this extinct family are intermediate in structure between those of the *Suidæ* and *Anthracotheriidæ;* having in the upper jaw very broad and short crowns, which carry five columns arranged as in the latter family. The premolars, although somewhat compressed, are not secant, and may be of very large size. In the two best known European genera there is a diastema between the first and second upper premolars. The mandible has no descending flange at the angle.

One of the most pig-like members of this family is the genus *Cebochœrus*, comprising animals of the size of *Hyotherium*, which have been considered by some as allied to the *Lemuridæ*, although there is little doubt that their true relationships are with the present group. They apparently possessed the full typical number of teeth, which (especially in the lower jaw) present a great resemblance to those of *Hyotherium;* and it is highly probable that they are closely related to the ancestor of that genus. *Cebochœrus* is represented by several species in the Upper Eocene of France; but the form re-

corded from the Middle Miocene of Bavaria may be generically distinct. Allied to this genus are *Hemichœrus* of the Quercy Phosphorites, and *Leptochœrus* of the North American Miocene, in which the premolars have a very simple structure. All these forms, together with the following genus, are placed by some writers with the *Suidæ*. The type genus *Chœropotamus* occurs in the Upper Eocene of France and England, and has been erroneously stated also to occur in the Miocene of Bavaria. The upper true molars resemble those of certain species of *Anthracotherium*, but have shorter crowns, with a less approach to a selenodont structure. There is a third lobe to the last lower true molar, and the dental formula is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{4}{3}$, $M.\frac{3}{3}$. The feet are unknown, but it is probable that they were furnished with four digits. The type species *C. gypsorum* of the Paris gypsum, was an animal of the size of a large Pig; and it is probable that this genus is a survivor of a form which was the common ancestor of both the *Suidæ* and the *Anthracotheriidæ*. *Elotherium*, which has been also described under the names of *Entelodon*, *Archæotherium*, *Oltinotherium*, and *Pelonax*, is a larger form allied in many dental characters to *Chœropotamus;* and is one of the very few members of this suborder in which the last lower true molar has no third lobe. The premolars are relatively large and simple; the canines recall those of some of the Carnivora; and the functional digits of the feet are reduced to two. The dental formula is the typical one; and the genus is placed by some writers in the *Anthracotheriidæ*. Its remains are found in the Upper Eocene Phosphorites of Quercy, in the Lower Miocene of Ronzon, in France, and of Hempstead in the Isle of Wight, and also in the Miocene of North America. Apparently allied to this genus is *Tetraconodon* of the Pliocene of the Indian Siwalik Hills, in which the last lower molar has a third lobe, and the conical premolars are of enormous size. In this neighbourhood must probably also be classed the remarkable North American Eocene genus *Achænodon* (probably identical with *Parahyus*) which has, however, been considered by Professor Cope as allied to the Lemuroidea and Insectivora. The structure of the teeth is like that obtaining in the present family, and the last lower molar has a third lobe, but the first premolar is wanting in both jaws. The skull presents, however, several Carnivorous features, and it is possible that this genus should rather be placed among the bunodont Condylarthra in the neighbourhood of *Periptychus*. The resemblance presented by the teeth of the latter to those of *Elotherium* and *Achænodon* is, indeed, so remarkable as to suggest that those two genera may be descendants of some unknown member of the Condylarthra very closely allied to the *Periptychidæ*.

Family Anthracotheriidæ.—In this family the dental formula is, with one exception, *I.* $\frac{3}{3}$, *C.* $\frac{1}{1}$, *Pm.* $\frac{4}{4}$, *M.* $\frac{3}{3}$; the upper true molars (fig. 1199) have broad, low crowns, with five columns, three of which are situated on the anterior and two on the posterior lobe; the columns in both upper and lower molars have a more or less distinctly selenodont structure; and the mandible has a descending flange at the angle. The Anthracotheres were probably in appearance somewhat between a Pig and a Hippopotamus, and doubtless dwelt in swamps and marshes. In the type genus *Anthracotherium* (fig. 1197) the selenodont structure of the teeth is less marked than in the next genus, with which it agrees in having four digits to each foot.

The species which approaches nearest to *Chœropotamus* in the structure of its molars is the small *A. silistrense* of the lower Siwaliks of India; but the still smaller *A. Gresslyi* (fig. 1197) from the Upper Eocene of Switzerland and Hampshire, agrees with that genus in having a diastema

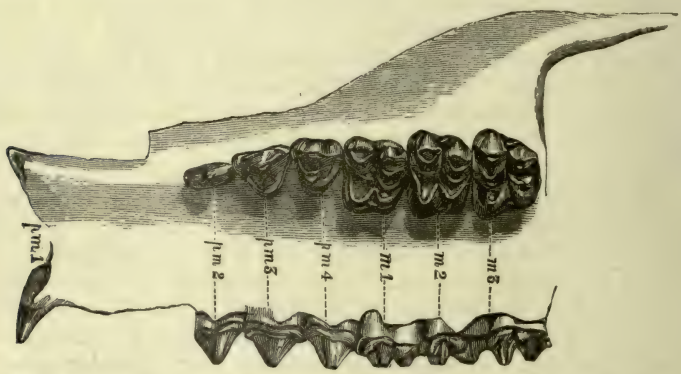


Fig. 1197.—*Anthracotherium Gresslyi.* The left half of the palate and the upper cheek-dentition; from the Upper Eocene of Hordwell, Hampshire.

between the first and second upper premolars, and in the absence of the first lower premolar. In most of the other species all the cheek-teeth were in contact. This genus commenced in the Middle Eocene of Promina in Dalmatia, where it is represented by *A. dalmatinum*, which has been made the type of the genus *Prominatherium;* it was abundant in the Quercy Phosphorites and Lower Miocene of Europe, where it was represented by species like *A. magnum*, *A. valdense* of Lausanne, and *A. illyricum* of Tuscany, which attained the size of a Rhinoceros. It was represented in the Middle Miocene of France by *A. Cuvieri*, after which it died out in Europe, although it survived in India till the Upper Miocene, where it is known by the large *A. hyopotamoides* and the small *A. silistrense.* It is unknown in America.

The genus *Hyopotamus* generally has a more completely selenodont dentition than *Anthracotherium*, but in some species (fig. 1198) these characters are less marked, and thus indicate a complete transition between the two genera. In those species (fig. 1199) which have the most perfectly selenodont dentition the columns of

Fig. 1198.—The third left upper true molar of *Hyopotamus giganteus*. Upper Miocene, India.

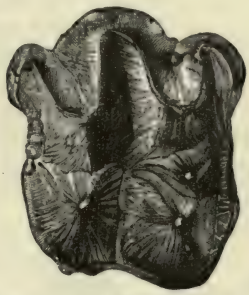


Fig. 1199 — The third right upper true molar of *Hyopotamus bovinus*. Lower Miocene, Isle of Wight.

the true molars are taller than in the others. The first upper premolar is separated by an interval both from the canine and the second premolar. This genus apparently commenced in the Upper Eocene of Europe, and is especially characteristic of the Hempstead beds of the Isle of Wight, and of the Ronzon beds of France, where it is represented by the large *H. bovinus* (fig. 1199), *H. velaunus*, and the brachydont *H. porcinus*. In India it survived till the Upper Miocene, where it is represented by two species, one of which (fig. 1198) is the largest known form; it also occurs in the Miocene of North America. The name *Diplopus* has been applied to a form from the Upper Eocene of Hampshire, with only two digits to each foot, which has been referred to this family; since, however, its dentition is unknown this determination is only provisional, and it has been suggested that it may be a *Dichodon*, although it appears too large for the type species.

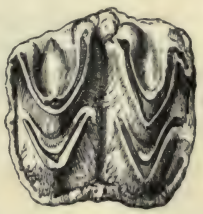


Fig. 1200.—A right upper true molar of *Merycopotamus dissimilis*; from the Pliocene of India.

Family Merycopotamidæ. — This family may be regarded as an offshoot from the *Anthracotheriidæ* in which the upper true molars (fig. 1200) have only four columns on their crowns; the dental formula being the same. It is probable that the feet were tetradactylate; and the mandible

has a descending flange. Some writers include this family in the *Anthracotheriidæ*, and perhaps this is really the better arrangement. The type genus is found only in the Pliocene Siwaliks of India and Burma, where it is represented by *M. dissimilis* (fig. 1200), and two smaller species. An imperfectly known but closely allied form from the Upper Miocene of Sind has been described under the name of *Hemimeryx*. In this and all the preceding families the odontoid process of the axis vertebra is peg-shaped.

Family Cotylopidæ.—This extinct North American family, usually known as the *Oreodontidæ*,[1] is regarded by Professor Cope as related to the *Anoplotheriidæ*, but with more completely selenodont teeth and less specialised feet, which are more like those of the Hippopotamus than those of the Ruminants; but their affinities are probably widely spread. Upper incisors are present; the true molars (fig. 1201) are selenodont, and those of the upper jaw usually have only four columns on their crowns; and the pre-

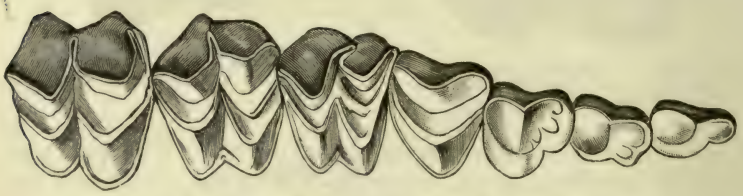


Fig. 1201.—Oral surface of the right upper cheek-teeth of *Eporeodon major*. Miocene, North America.

molars are simpler than the true molars, but are not secant. The lower canine is approximated to the incisors, and its function is taken by the first premolar, which has a tall crown biting behind the upper canine. The ulna, radius, tibia, fibula, metapodials, navicular, and cuboid are all distinct; and each foot carries four digits. The odontoid process of the axis vertebra is intermediate in shape between the peg of the Bunodonts and the half-cylinder of the Ruminants; the lachrymal bone frequently has a deep *larmial* depression; but the angle of the mandible has no descending flange.

In the type genus *Cotylops* (*Oreodon*) the dentition is $I.\ \frac{3}{3}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{4}{4}$, $M.\ \frac{3}{3}$; the orbits are completely surrounded by bone, the premaxillæ are separate, the auditory bullæ not inflated; there are no vacuities in the bones of the face; and there is a small pollex in

[1] The name *Oreodon* being preoccupied by *Orodus* (*supra*, p. 940), involves the change of the family name. *Cotylops* was originally applied by Leidy to one species of the type genus.

the manus. In *Eporeodon*, or *Eucrotaphus*, the above characters are the same, with the exception that the tympanic bullæ are inflated; while *Merycochœrus* differs from the latter by the anchylosis of the premaxillæ. There are seven species in the latter genus. *Merychyus* is distinguished from *Merycochœrus* by the presence of vacuities in the lachrymal region. In *Leptauchenia*, which has been placed by some writers in the *Camelidæ*, such vacuities occur

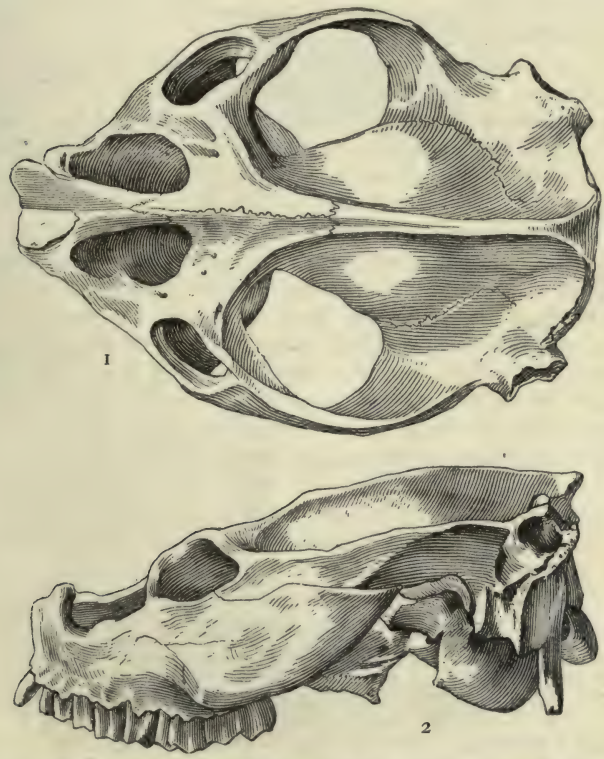


Fig. 1202.—Frontal (1) and left lateral (2) aspects of the cranium of *Cyclopidius emidinus*; from the Miocene of the United States. Reduced. (After Cope.)

close to the frontals, and the nasals become very small. Still more remarkable is the enormous development of these vacuities in *Cyclopidius* (fig. 1202), in which the upper incisors are wanting. *Pithecistes*, again, differs from all the preceding by the absence of the first premolar, and has but one pair of lower incisors. In the second division of this family, which includes the genera *Agriochœrus* and *Coloreodon*, the orbit is incompletely surrounded by bone, and the

fourth upper premolar has two outer columns in place of the single one of the typical section (fig. 1201). *Coloreodon* differs from *Agriochœrus* by having only three premolars, but it may be questioned whether this difference really affords sufficient grounds for generic distinction. The majority of the genera are confined to the White River Miocene of North America, but *Merycochœrus* extends into the Loup-Fork beds, which may be either of Upper Miocene or Lower Pliocene age. A tooth, apparently indistinguishable from the molars of *Agriochœrus*, has been obtained from the Pliocene of India.

Here may be noticed a remarkable form from the Upper Eocene of the United States, described under the name of *Protoreodon*. The organisation is said to be of the Cotylopine type, but the upper molars have five columns, as in the *Anthracotheriidæ* and *Anoplotheriidæ*. This genus probably indicates an ancestral type of the *Cotylopidæ*, which should perhaps be referred to a distinct family; it is, however, placed by Professor Cope near the Xiphodonts.

Family Anoplotheriidæ.—In this family the cheek-teeth are imperfectly selenodont; the crowns of the upper true molars (fig. 1204) carrying five columns, three of which are placed on the anterior, and two on the posterior lobe, or half, of the crown. All the bones of the limbs and feet remain distinct from one another; and there is no descending flange at the angle of the mandible. The functional digits may be either two or three in number; and the carpus and tarsus of the original genus are of that type to which the name inadaptive has been applied.[1] The anterior premolars are more or less perfectly secant; there is generally no diastema in the dental series; and the canines are short and compressed, and depart very widely from those of the *Anthracotheriidæ* and their allies, in which they resemble the corresponding teeth of the Carnivora. In the type genus *Anoplotherium* (in which may be included *Eurytherium* and *Diplobune*) the dentition (fig. 1204) is usually $I.\ \frac{3}{3}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{4}{4}$, $M.\ \frac{3}{3}$; but occasionally the first lower premolar is wanting. The tail (fig. 1203) is long; the functional digits may be either three or two;[2] and the third upper premolar has a well-developed inner tubercle. In the typical *A. commune*, of the

[1] In the inadaptive modification (*Anoplotherium*) the carpals of the aborted digits remain as useless lateral bones; while in the adaptive modification (*Hyotherium*) they shift their position, and take a share in the support of the large persistent digits.

[2] Prof. Cope has suggested that the forms with two digits should be excluded from this family, but it is the type species which presents this feature. The form with three functional digits is indistinguishable by dental characters from the typical *A. commune* with only two.

Paris gypsum, the columns of the cheek-teeth are comparatively tall, but in other species, like *A. cayluxense* of the Quercy Phosphorites (fig. 1204), they are shorter, and the teeth thus approximate to those of the brachydont species of *Hyopotamus*. This genus is confined to Europe, and is characteristic of the Upper Eocene (Lower Oligocene) and the Miocene of Ronzon in Puy-en-

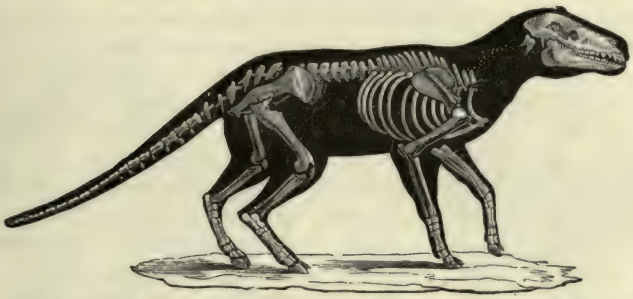


Fig. 1203.—Skeleton of *Anoplotherium commune;* Upper Eocene, Europe. Much reduced

Velay. The species from the South American Tertiaries originally referred to this genus is now known as *Proterotherium*, and is noticed under the Perissodactyla. The largest species was about the size of a Tapir. Here may be noticed five genera from the Quercy Phosphorites, some of which appear, on the whole, to be most nearly allied to *Anoplotherium*, although their teeth present certain resemblances to those of the Perissodactyla, in which suborder the last of the group is placed by some writers. Of these

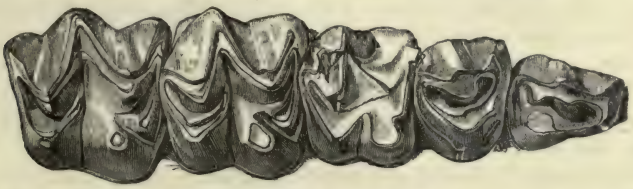


Fig. 1204.—The last five right upper cheek-teeth of *Anoplotherium cayluxense;* from the Upper Eocene of France.

genera *Adeotherium* is characterised by the extreme complexity of the last upper premolar, which resembles the first true molar; *Metriotherium* is only known by the mandible, in which the premolars are simpler than in the type genus; and the true molars show some resemblance to those of *Lophiomeryx; Mixtotherium*, which is described from the palate, and is probably identical with

the preceding, also has simple premolars; *Myxochœrus* shows less completely selenodont teeth; while those of *Tapirulus* approximate to the molars of the *Tapiridæ*. In another direction we have *Dacrytherium* and *Plesidacrytherium*, from the Upper Eocene of France and England, in the former of which the first upper incisors of either side are separated from one another by a wide interval, while the first three premolars are more completely secant than in the type genus. The dental type of *Dacrytherium* leads on closely to that of *Xiphodon*, which, in accordance with the views of Professor Rütimeyer, is therefore placed in the same family, although some writers make it the type of another family, which is taken to include either *Cœnotherium* (Flower), or *Dichodon* (Schlosser). The true molars are like those of the type genus *Anoplotherium*, although more completely selenodont; but the first three premolars (fig. 1205) are much elongated and compressed; and the functional digits were reduced to two in each foot. In the typical forms there was no diastema in the dental series (which comprises the full typical number), but in certain smaller forms, separated by some writers under the name of *Xiphodontotherium*, a distinct diastema was developed. The Xiphodonts were animals of slender build, with limb-bones partly resembling those of *Anoplotherium*, and partly those of the more specialised Selenodonts; they are characteristic of the Upper Eocene of England and the Continent, the largest species being *X. magnus*, and the smallest *X.* (*Xiphodontotherium*) *secundarius*, of the Quercy Phosphorites. This genus, although not in the direct line, shows how a transition can be effected from the higher *Anthracotheriidæ* to the *Dichodontidæ*. *Rhagatherium*, from the Upper Eocene of Switzerland, is an allied genus. Finally, Dr Ameghino refers to this family the genus *Brachytherium*, from the Tertiary of South America; while Dr Schlosser would include in it the genus *Tetraselonodon*, founded on teeth from the Quercy Phosphorites, which have only four columns on the crown.

Fig. 1205.—The last two left upper premolars and first true molar of *Xiphodon gracilis*; from the Upper Eocene of Hampshire.

Family Cænotheriidæ.—Following the classification of Professor Rütimeyer the next family we have to consider is that of which the type genus is *Cœnotherium*. All the genera have the full complement of teeth, and there are usually five columns, or cusps, on the crowns of the upper true molars (which may be either selenodont or bunodont); two of these columns being placed on the anterior and three on the posterior lobe of the teeth, thus reversing the arrangement obtaining in the *Anoplotheriidæ*. The type genus *Cœnotherium* comprises a number of species of small animals not

larger than a Rabbit, in which the teeth are selenodont; the anterior premolars more or less secant; the auditory bullæ inflated (fig. 1206) and the feet furnished with four complete digits. These small animals probably approximated in outward appearance to the living Chevrotains (*Tragulus*) of the Oriental region. In the typical forms there is no diastema in the dental series; but this is present in other species to which the name *Plesiomeryx* has been assigned

Fig. 1206.—*Cænotherium Filholi.* Upper and lower views of the cranium; from the Upper Eocene of Caylux.

by some writers. The limb-bones show characters connecting them both with the *Suidæ* and the Ruminants. In the figured cranium the nasals are peculiar for terminating in a point. This genus, of which the names *Zooligus* and *Microtherium* are also synonyms, ranges from the Upper Eocene (Lower Oligocene) of Vaucluse to the Lower Miocene (Upper Oligocene) of Allier. An allied genus is *Mouillactherium*, of the Quercy Phosphorites, in which the third upper true molar has but four columns; while yet another allied form from the same deposits has received the name *Oxacron.* The European Upper Eocene genus *Dichobunus* (*Didymodon*) is regarded by Professor Rütimeyer as a bunodont form closely allied to *Cænotherium; Dilotherium* and *Spaniotherium* being kindred genera

from the Quercy Phosphorites. The limb-bones, although all the four digits are developed, show considerable resemblances to those of the Ruminants, and it has been thought that *Dichobunus* may have been the direct ancestor of *Gelocus*. Here also may be mentioned the peculiar Upper Eocene European genus *Acotherulum*, in which the general form of the skull and teeth of the one known species seems to indicate affinity with *Dichobunus*, while the absence of the third cusp on the hinder lobe of the upper true molars, and the more completely bunodont structure of these teeth apparently indicates affinity with *Cebochœrus* and its allies, among which some writers prefer to place this genus.

Family Dichodontidæ.—According to the views of Professor Rütimeyer this family is taken to include several genera with a selenodont dentition in which the upper true molars have four columns; the type genus *Dichodon* presenting affinities with *Xiphodon*, while *Gelocus* and its allies are closely related to the *Tragulidæ* and the *Cervidæ*. Other writers, however, who do not attach such importance to the structure of the molars, place *Dichodon* with *Xiphodon* and make *Gelocus* the type of a distinct family.[1] In *Dichodon* the dental formula is $I.\ \frac{3}{3},\ C.\ \frac{1}{1},\ Pm.\ \frac{4}{4},\ M.\ \frac{3}{3}$; the upper true molars having concave outer surfaces somewhat like those of *Hyopotamus*, while the earlier premolars are elongated and secant, and thus approach those of *Xiphodon;* there is no diastema. The limb-bones are unknown, but it is probable that there were only two functional digits. This genus occurs in the Upper Eocene of Hampshire. In *Lophiomeryx* (fig. 1207) from the Upper Eocene and Lower Miocene of the Continent, the hinder inner crescent of the upper true molars is imperfectly developed, and the first lobe of the lower true molars resembles that of *Anoplotherium*, while the second is Ruminant-like. The lower molars also resemble those of *Metriotherium* (p. 1329), and the family position of this genus, which is referred by Prof. Cope to the *Tragulidæ*, is still doubtful. *L. Gaudryi* from the Quercy Phosphorites has been made the type of the genus *Cryptomeryx*. In *Gelocus*, from the Quercy Phosphorites and Lower Miocene of Puy-en-Velay, it is not known whether upper incisors were present;

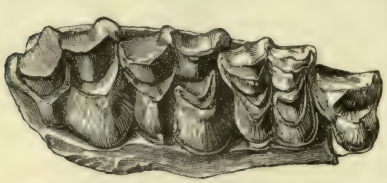


Fig. 1207.—The last four right upper cheek-teeth of *Lophiomeryx Chalaniati*; from the Quercy Phosphorites.

[1] Prof. Cope would include in this family the type genus and the American *Agriochœrus* and *Coloreodon*.

but the upper molars have low columns, with wide and open valleys, the external surface of each lobe resembling that of *Dichodon*. The navicular and cuboid bones of the tarsus were united, and the metatarsals fused into a cannon-bone, although the metacarpals were distinct. Allied to this genus are *Phaneromeryx* and *Protomeryx* of the Upper Eocene of France; while *Chæromeryx* of the Siwaliks of India may be provisionally referred to this family.

Family Tragulidæ.—The fossil forms included in this family indicate a transition from the typical genus on the one hand to the *Dichodontidæ*, and on the other to the *Cervidæ*. The upper true molars have four columns, and the earlier premolars are more or less completely secant. None of the genera were furnished with antlers, and it is probable that upper incisors were likewise always absent. In the existing forms the upper canines of the males (fig. 1208) are in the shape of tusks; there is a long diastema in both jaws; the third stomach, or 'psalterium,' is wanting; and the placenta is diffuse. The feet have supplementary toes, and the metacarpals of the third and fourth digits either unite late in life to form a cannon-bone, or remain (as in *Hyomoschus*) permanently separate. *Bachitherium* of the Quercy Phosphorites, in which there are three premolars in each jaw, shows resemblances both with *Gelocus*, *Hyomoschus*, and *Prodremotherium;* the upper teeth being very similar to those of the latter. In *Dorcatherium*, with which the existing *Hyomoschus* of Africa appears generically identical, the premolars are $\frac{3}{(3-4)}$, and are of a secant type, and thus indicate affinity with the *Dichodontidæ;* this genus is found in the Middle Miocene and Lower Pliocene of the Continent, and also in the Pliocene of India. *Tragulus*, which differs by the fusion of its metapodials into cannon-bones, and by never having more than three lower premolars, is now confined to the Oriental region, and is represented by one species in the Pliocene of India. *Leptomeryx*, from the Miocene of North America, has four premolars, of which the first three are simply secant as in *Tragulus*, while the fourth has an inner tubercle; there are four separate metacarpals, but the third and fourth metatarsals form a cannon-bone, as in *Gelocus*. In *Prodremotherium*, of the Quercy

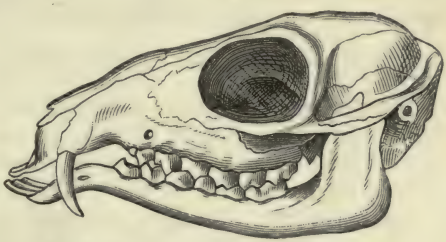


Fig. 1208.—Reduced side view of the skull of *Tragulus javanicus*.

Phosphorites, the dentition is almost, if not quite, indistinguishable from that of *Leptomeryx*, but cannon-bones are found in both limbs, although the union of the factors in the anterior ones is less complete than in the others. These two genera apparently connect *Gelocus* so completely with the cervine *Palæomeryx*, that we can have no hesitation in regarding them as representing the direct line of the descent of the *Cervidæ* from the *Dichodontidæ;* while we must consider the existing *Tragulidæ* as lateral offshoots from some nearly allied primitive stock. *Hypertragulus*, from the Miocene of North America, appears to be a form closely allied to *Leptomeryx*, but with the metatarsals separate.

Family Poëbrotheriidæ.—We must here leave for a short time the connection between the *Tragulidæ* and the *Cervidæ*, to consider the Camels and their allies, whose nearest existing relations are to be found in the former family. The *Poëbrotheriidæ* are represented typically by the genus *Poëbrotherium*, of the North American Miocene, in which the dental formula is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{4}{4}$, $M.\frac{3}{3}$. The structure of the cheek-teeth is selenodont; in the feet the third and fourth metacarpals remain distinct, the second and third being rudimentary; the carpus has a trapezium; and the navicular and cuboid are not fused together. The structure of the cervical vertebræ is the same as in the *Camelidæ*, of which this family may be regarded as the ancestral type; but in other respects there are signs of affinity with the *Tragulidæ*. The type species of *Poëbrotherium* was scarcely larger than a Fox. In the John Day Miocene of Oregon an allied form has received the name of *Gomphotherium;* while *Leptotragulus* of the Upper Eocene of the United States may be the ancestral form of both the Miocene genera.

Family Camelidæ.—In the Camels the cheek-teeth are selenodont and quadricolumnar, but of somewhat simpler structure than those of the following families. The navicular and cuboid remain distinct, but the metapodials unite to form a cannon-bone. At least one pair of upper incisors is present; and in the cervical vertebræ the arterial canal passes obliquely through the anterior part of the pedicle of the neural arch, and is thus confluent posteriorly with the neural canal; a similar condition prevailing in *Macrauchenia* among the Perissodactyla. At the present day this family is represented by *Camelus* of the Old, and *Auchenia* of the New World; but it appears to have originated in the latter, where a large number of forms have been found. The most generalised member is *Protolabis*, of the Miocene of the United States, in which the dentition is numerically the same as in *Poëbrotherium*, on which grounds Professor Cope makes it the type of a distinct family. In *Procamelus* (fig. 1210, B, C) of the Lower Pliocene or Upper Miocene

of the same area, the incisors were reduced (as in all the other forms) to $\frac{1}{3}$, but there were still four premolars, although the first is isolated and the second very small. *Pliauchenia* (which is perhaps identical with *Homocamelus*) has only three lower premolars, and occurs in the

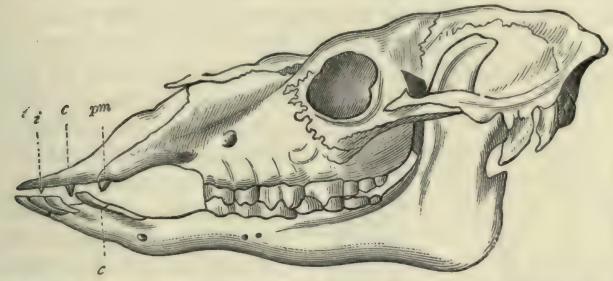


Fig. 1209.—Left lateral view of the skull of the Camel (*Camelus bactrianus*). Reduced. *i*, Upper incisor; *c*, *c*, Canines; *pm*, Isolated premolar. The maxillo-premaxillary suture should have been placed in front of *c* instead of in front of *pm*.

Loup-Fork-beds of North America. In *Camelus* again (fig. 1209) the normal adult formula of the cheek-teeth is *Pm.* $\frac{2}{3}$, *M.* $\frac{3}{3}$; the first upper premolar being canine-like, and separated by a long interval from the penultimate tooth of that series. This genus is confined to the Old World; the earliest known species occurring in the Pliocene of India, and another form (*C. Thomasi*) in the Pleistocene of Algeria. The molars of the Siwalik species show characters now only found in *Auchenia*. The latter generic term is here taken

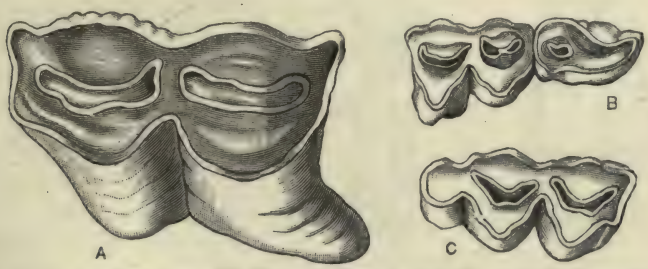


Fig. 1210.—A, First left lower true molar of *Auchenia hesterna*, Pleistocene, California; B, Fourth right upper premolar and first true molar of *Procamelus virginiensis*, Miocene, North America; C, Third right lower true molar of do.

to include a number of fossil New World forms some of which have been generically separated under the names of *Hemiauchenia*, *Palauchenia*, *Protauchenia*, *Holomeniscus*, and *Eschatius*. In the

existing species, which occur fossil in the caves of Brazil, the premolars are normally $\frac{2}{2}$ in number, but there is often but one of these teeth in the lower jaw; in *A.* (*Palauchenia*) *magna* from the Pleistocene of Mexico, there were always two and occasionally three lower premolars; while in a Pleistocene South American species (*Hemiauchenia*) there were three premolars in both jaws. In *A.* (*Holomeniscus*) *hesterna* (fig. 1210, A), from the Pleistocene of North America, on the other hand, the premolars were reduced to one in each jaw; while *A.* (*Eschatius*) *vitakeriana* has the same number, but is distinguished by the simpler nature of the upper one. The majority of the species were of comparatively small size, but *A. magna* and *A. hesterna* were equal in bulk to the Camels of the present day.

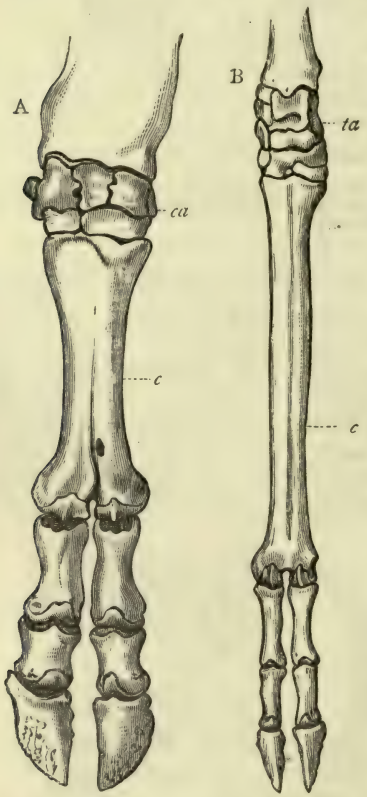


Fig. 1211.—A, Dorsal aspect of the right manus of Ox (*Bos taurus*); B, Do. of right pes of Red-Deer (*Cervus elaphus*). Reduced. *ca*, Carpus; *ta*, Tarsus; *c*, Metapodium (cannon-bone).

Family Cervidæ.—The present and three following families of the suborder collectively constitute the Pecora of recent Zoology;—a group well defined at the present day, but, as already mentioned, connected in past epochs most intimately by this family with the *Tragulidæ*. The dentition of the entire group is usually $I.\frac{0}{3}$, $C.\frac{(0-1)}{1}$, $Pm.\frac{3}{3}$, $M.\frac{3}{3}$; upper incisors being invariably absent. The true molars are perfectly selenodont, and the upper ones carry four columns; the second premolar is always in contact with the third; there is a long interval, or diastema, between the lower premolars and canine; and the latter is approximated to, and closely resembles the incisors. The third and fourth metapodials (fig. 1211) coalesce into a cannon-bone; the navicular and cuboid of the tarsus are likewise united; and the odontoid process of the axis vertebra forms a spout-like

half-cylinder. Moreover, in all existing members of this group the lateral metapodials are either incomplete or totally wanting (fig. 1211); the stomach is composed of four complete cavities; and the placenta develops structures known as cotyledons. On the skull either horns or antlers are very generally present, at least in the males of recent forms.

In the *Cervidæ* upper canines are generally present, although with a few exceptions they are of comparatively small size; the cheek-teeth, and more especially in the earlier forms, are very generally of a more or less brachydont structure, the first true molar being invariably of this type; and the upper premolars always have both an inner and an outer column, and are never simply secant like those of the existing *Tragulidæ*. In the skull there is always a large vacuity in front of the lachrymal, which prevents that bone from articulating with the nasal. In a large number of forms antlers are present in the male, and in *Rangifer* also in the female. Antlers, it may be observed, are outgrowths of true bone arising from the frontal

Fig. 1212.—Reduced left lateral aspect of the skull of the Roebuck (*Capreolus caprea*).

region of the skull (fig. 1212), which during their development are invested with a vascular, hairy skin. On the completion of their growth a constriction of the blood-vessels near their base is usually brought about by the formation of a *burr*, and above this point the skin peels off and leaves the bone bare and insensible; after a time the antler is shed, leaving a more or less elongated pedicle attached to the skull, from which a new antler is developed. In young animals the antlers are simple, and in those species in which they finally attain a great complexity, this is acquired gradually in successive annual growths. Each antler always consists of a main stem or *beam*, and usually of one or more branches or *tines;* of which the one immediately above the burr

is termed the *brow*-tine. The lateral digits are nearly always present, and the distal extremities of the metapodials may be preserved. The existing Deer have been divided into the Plesiometacarpalia (*Cervus* and *Cervulus*), and the Telemetacarpalia (*Alces*, *Capreolus*, *Cariacus*, and *Rangifer*); the former, which mainly inhabit the Old World, characterised by the retention of the proximal, and the latter of the distal extremities of the lateral metacarpals. As in many analogous instances, the development of the antlers of the individual is paralleled by their development in the family; since we find that many of the earlier members were totally unprovided with these appendages, and that their extreme complexity in the more specialised forms was not acquired until a late period in the geological scale.

The least specialised members of this family form the closely allied extinct genera *Amphitragulus* and *Palæomeryx*. In the former there are four lower premolars, and antlers were entirely absent; the crowns of the molars being low. The largest species was somewhat bigger than the Musk-Deer, and the genus is characteristic of the Lower Miocene of the Continent. *Palæomeryx* (*Dremotherium*, *Dicroceros*, and *Micromeryx* being included) has only three lower premolars, except in one species; and the upper true molars (fig. 1213), like those of *Amphitragulus*, were brachydont, and had no distinct accessory column between the inner crescents. In one species (*P. Feignouxi*) the lateral metacarpals were perfect, although very slender, and the males had long upper canines like those of the Musk-Deer, but no antlers; this species being the earliest, and occurring in the Lower Miocene of France. In *P. furcatus* (*Dicroceros elegans*), of the Middle Miocene, simple antlers were, however, present, and the canines were apparently small. *P. Bojani*, of the French Middle Miocene, and *P. sivalensis* (fig. 1213), of the Pliocene of India, were as large as a Red Deer; and the latter species, together with another from the Pliocene of China, were the last representatives of the genus, of which the latest appearance in Europe is in the Middle Miocene of Sansan, in France. *Platyprosopus*, from the latter beds, is distinguished by the great projection of the angle of the mandible. To the existing Oriental genus *Cervulus*, in which the molars are more hypsodont, and simple antlers mounted on a long pedicle are present, may be provisionally referred *C. dicranoceros* (fig. 1214, A), of the Pliocene of Eppelsheim. There is some uncertainty as to the earliest appearance of the genus *Cervus*, but it not improbably dates from the Middle Miocene, and was abundant

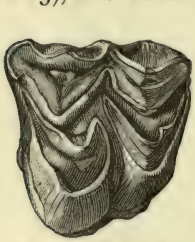


Fig. 1213. — Left upper true molar of *Palæomeryx sivalensis*. Pliocene, India.

in the Lower Pliocene; at the present day it ranges throughout the Palæarctic region, but is unknown in the Ethiopian region and the greater part of America. This genus, as we have already observed, belongs to the Plesiometacarpalian section; the antlers may be of

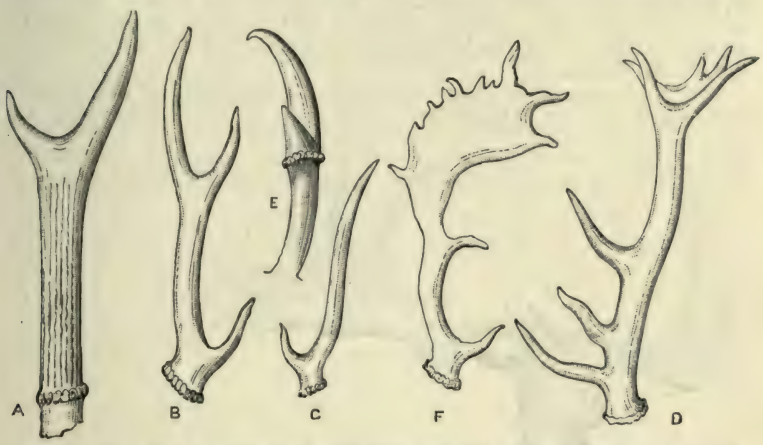


Fig. 1214.—A, Antler of *Cervulus* (?) *dicranoceros*—Pliocene; B, Antler of *Cervus pardinensis*—Pliocene; C, Antler of the Red Deer (*Cervus elaphus*) in the second year; D, Antler of the same in its fully-grown condition; E, Antler and bony pedicle of the frontal bone of the Muntjak (*Cervulus muntjak*); F, Antler of the Fallow Deer (*Cervus dama*).

extreme complexity; and the hinder molars are either brachy- or hypsodont, there being frequently an inner accessory column in the upper true molars.

The genus is divided into a number of groups, of which the distribution can only be briefly noticed. The most aberrant is the *Tetracerotine* group, formed by *Cervus tetraceros* of the French Pliocene, in which the antlers approximate to those of *Cariacus*. The *Axine* group, now confined to the Oriental region, in which the molars are more hypsodont than usual, and the antlers are rounded and comparatively simple, is represented by several species, such as *C. pardinensis* (fig. 1214, B), in the Pliocene of Europe, while the living *C. axis* occurs in the Pleistocene of Madras. The Oriental *Rucervine* group has a representative in *C. sivalensis*, of the Pliocene of India; while the allied *Rusine* group, of the same region, in which the antlers are still comparatively simple, and with their beam often strongly grooved, is known in a fossil state by the remains of existing species from the Pleistocene of India. In the *Elaphine* group, which includes the Canadian Wapiti (*C. canadensis*), the Red Deer (*C. elaphus*) of Europe and North Africa, together with some large species from the Palæarctic region, the antlers (fig. 1214, C, D), although still rounded, are often cupped at their summits, and carry a second, or *bez-tine*, immediately above the brow-tine. In this group remains referable to the existing Red Deer (*C. elaphus*) are of common occurrence in the Pleistocene of Europe. Some of the fossil antlers and jaws indicate, however, much larger animals than any Red Deer now existing,

and it has been suggested that these remains belong either to *Cervus maral* of Persia, or to the Wapiti (*C. canadensis*) of North America. Both these forms are, however, closely allied to the Red Deer, and it appears preferable to regard all the European fossils as referable to a single species from which the three existing types are derived. There is, however, the name *C. spelæus* for the large fossil form (which is of earlier date than the name *C. maral*), if that be really distinct from *C. elaphus*. Remains of the Wapiti are recorded from the Pleistocene of the United States.

The *Eucladocerotine* group comprises *C. Sedgwicki* of the Norfolk Forest-bed and the Upper Pliocene of Italy, in which the antlers are

Fig. 1215.—Skeleton of the Irish Deer (*Cervus giganteus*); from the Pleistocene of Ireland. Greatly reduced. (After Owen.)

more complex than in any other species. In the *Damine* group the antlers (fig. 1214, F) have their terminations palmated, and the brow-tine simple; the existing Fallow-Deer (*C. dama*) occurs in the bone-caves of Gibraltar, while allied forms are found in the English Forest-bed and Crag; the most noteworthy being *C. verticornis*, in which the brow-tine

is bent sharply downwards. The last group which it is necessary to mention here is the *Megacerotine*, which contains only the Irish Deer (*Cervus giganteus*, fig. 1215), characterised by its enormous palmated antlers (fig. 1216), which diverge at right angles from the plane of the frontals, and have a distinct brow- (*Br*) and bez- (*Bz*) tine, and a small posterior tine (*PT*) on the opposite side of the beam to the bez-tine. Remains of this fine species are found in the Pleistocene of Northern Europe, and are especially abundant in the bogs of Ireland, where specimens have been found with a spread of more than eleven feet between the tips of the antlers.

Passing to the Telemetacarpalian genus *Rangifer*, which is at once characterised by the peculiar form of the antlers and their presence in both sexes, we find remains of the existing Reindeer (*R. tarandus*),

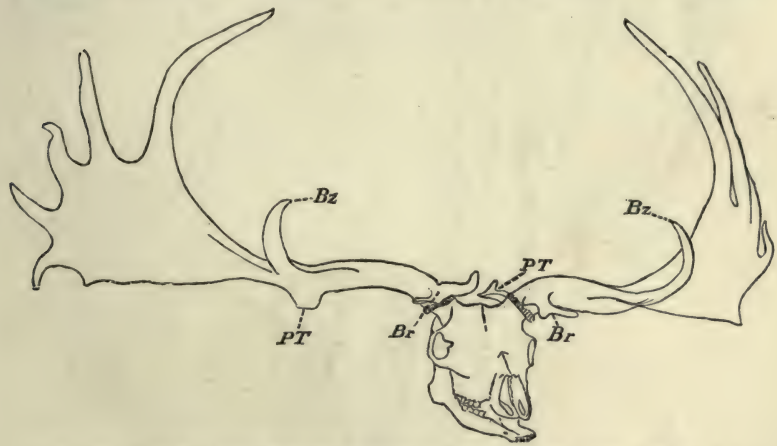


Fig. 1216.—Skull and antlers of *Cervus giganteus*. Reduced. *Br*, Brow-, *Bz*, Bez-, *PT*, Posterior tine. (After Scott.)

now confined to the higher latitudes of the Northern Hemisphere, abundant in the Pleistocene of a large portion of Europe. In *Alces* the Elk, or Moose (*A. machlis*), of the northern parts of Europe and America, occurs in the Pleistocene of the same regions; while an extinct species has been described from the Norfolk Forest-bed. The antlers (fig. 1217) have no bez-, and apparently no brow-tine, but are divided into an anterior forked branch (*A*) and a posterior palmated one (*P*). A very remarkable form from the Pleistocene of North America, described under the name of *Cervalces*, appears to connect *Alces* with *Cervus*, although it belongs clearly to the Telemetacarpalian section. Thus the antlers (fig. 1218) are superiorly divided into an anterior (*A*) and posterior (*P*) branch; but below the latter there occur two tines (*Bz* and *PT*), which Dr Scott regards as probably corresponding to the bez- and posterior tines

of the Irish Deer. And we may likewise trace an intermediate type in the vertical height of the skull, and the form and connections of the nasal and premaxillary bones. In *Capreolus*, where the antlers are simple and rounded, the existing Roe (*C. caprea*, fig. 1212) occurs in the European Pleistocene; while *C. cusanus*, of the French Pliocene, is regarded as the ancestor of that species; and the peculiar *C. Matheroni*, of the Lower Pliocene of both Greece and France, is provisionally referred to the same genus. *Cariacus*, again, which is peculiar to the New World, and is characterised

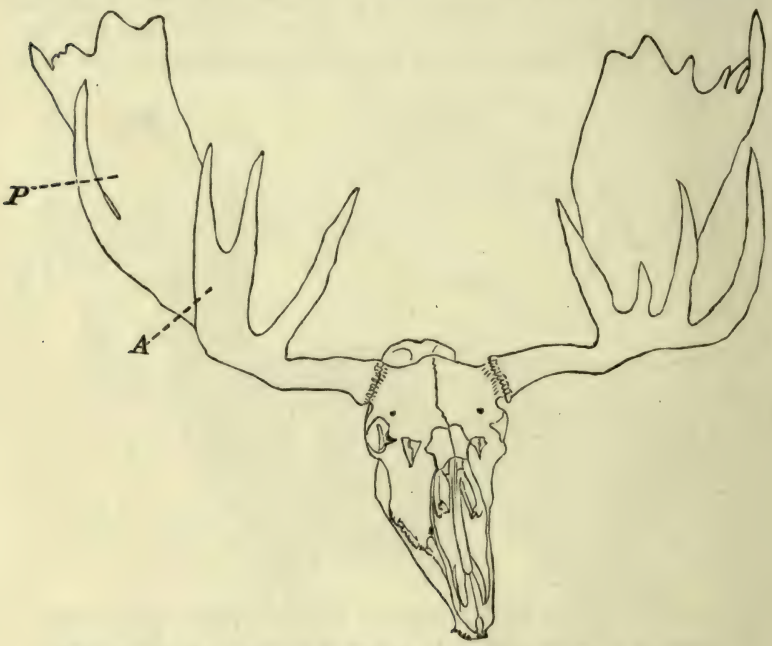


Fig. 1217.—Skull and antlers of the Elk (*Alces machlis.*) Reduced. *A*, Anterior; *B*, Posterior branch. (After Scott.)

either by very simple prong-like antlers, or by a more complex form totally unlike those of any existing members of the family, is represented by several existing, and perhaps by some extinct, species in the Pleistocene of South America. Lastly, it should be observed that antlered Deer occur in the Tertiaries of North America, and the name *Blastomeryx* has been applied to one form which is regarded as the ancestor of *Cariacus*.

All the preceding existing genera belong to the subfamily *Cervinæ*, but the Musk-Deer (*Moschus*), of the Himalaya and regions to the northward, is the type of a second subfamily—the *Moschinæ*. This

genus, in which there are no antlers, and the upper canines of the male attain an excessive development, not improbably occurs fossil in the Pliocene of the Siwalik Hills.

Family Giraffidæ.—In this family, which is taken to include the *Sivatheriidæ* of some authors, the cranial appendages, when present, appear to be intermediate in character between those of the *Bovidæ* and *Cervidæ*. The teeth are more or less brachydont, and invested with a rugose enamel; their number being *I.* $\frac{0}{3}$, *C.* $\frac{0}{1}$, *Pm.* $\frac{3}{3}$, *M.* $\frac{3}{3}$. The type genus *Giraffa* (*Camelopardalis*), which at the present day is represented only by *G. camelopardalis* of Africa, is closely allied to the *Cervidæ*, in which family it is included by Professor Rütimeyer; the frontal appendages consist of a pair of

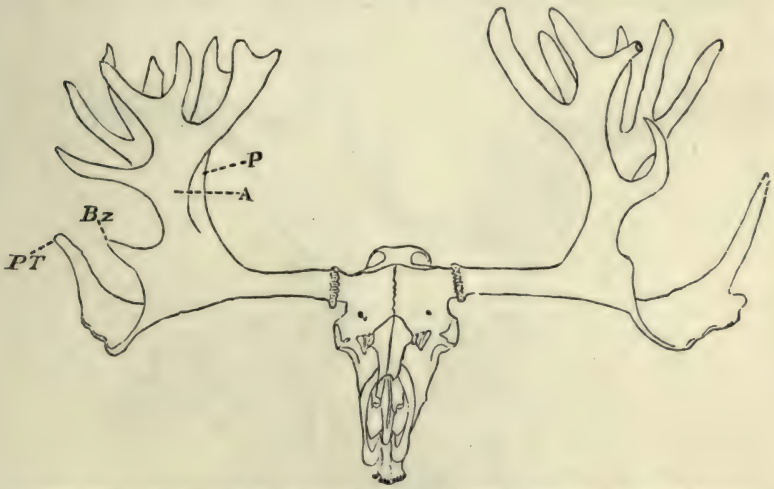


Fig. 1218.—Skull and antlers of *Cervalces americanus*; from the Pleistocene of North America. Reduced. Letters as in figs. 1216 and 1217. (After Scott.)

short, erect, bony processes, at first connected by suture, but subsequently anchylosed to the skull, which are covered with hairy skin, and are present in both sexes. Anteriorly to these there is a median process on the frontals and nasals, which is sometimes termed a third horn. There are no traces of lateral digits; the humerus has a double bicipital groove; there is a lachrymal vacuity in the cranium; and the neck and limbs are enormously elongated. Fossil species occur in the Lower Pliocene of Greece, Persia, India, and China. *Vishnutherium*, of the Siwaliks of Burma and India, appears to be an allied genus, with shorter limbs, but the

cranium is unfortunately unknown. The next place in the series is occupied by *Helladotherium*, of the Lower Pliocene of Greece, India, and perhaps Persia, in which the cranium is devoid of appendages, and the molar teeth become more like those of the Elk. The limbs are comparatively short and stout; the cranium has no lachrymal vacuity; and the one known species was of considerably greater bulk than the Giraffe. With *Hydaspitherium*, of the Pliocene of North-western India, we enter the group in which the cranium was provided with large branching antler-like appendages, although the exact nature of their covering is unknown. These appendages in this genus rise from a common base situated immediately in advance of the occiput, but their form is not known; there were lachrymal vacuities in the cranium. An apparently allied form, from the Pliocene of Persia, has been named *Urmiatherium*. In *Bramatherium*, of the Pliocene of Western India, there were two

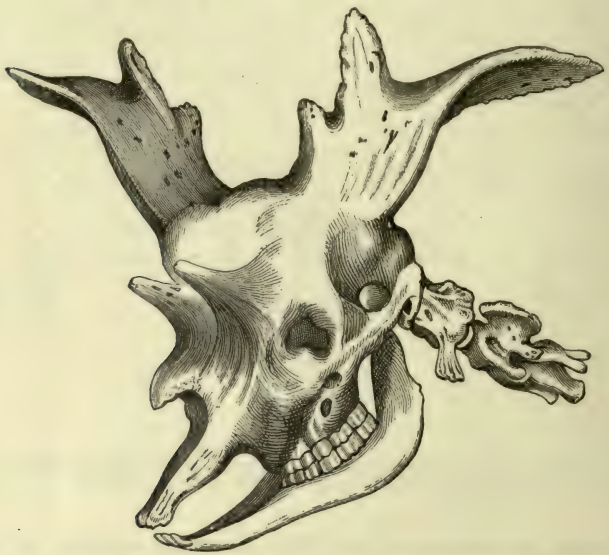


Fig. 1219.—Skull of *Sivatherium giganteum*; reduced. Pliocene, India. The position of the hinder antlers should probably be reversed.

pairs of these antler-like appendages, the anterior pair arising from a common base, and being of large size. Lastly, we have *Sivatherium* (fig. 1219), of the Pliocene Siwaliks of North-eastern India, in which the neck and limbs were not developed beyond the normal proportions. There are two pairs of cranial appendages, the bases of each being separate. The anterior pair are conical, like those of

the Giraffe; while the posterior ones are palmate, and resemble the antlers of the Elk. The latter pair are marked by the impressions of large blood-vessels, as in the *Cervidæ*, but do not show the burr characteristic of that family, from which it is inferred that they were not shed. There is no lachrymal vacuity in the cranium; the nasals are short and arched; and the bones of the skeleton approximate in structure to those of the *Cervidæ*. Some authorities regard this genus as most closely allied to brachydont Antelopes like *Strepsiceros*, but it appears to be so intimately connected with the preceding forms that it seems imperative to place it in the same family, although it may indicate an approximation to the *Bovidæ*.

The remarkable genus *Samotherium*, of the Lower Pliocene of the Isle of Samos, is referred by Dr Forsyth-Major to the present family, although its skull makes a remarkable approximation to that of the antelopoid genus *Palæotragus*. The females were hornless, but the males had a pair of small horns immediately above the orbit. The molars are described as being very like those of the Giraffe.

Family Antilocapridæ.—This family is now represented only by the American Prong-buck (*Antilocapra*), in which the horns are of the same nature as in the *Bovidæ*, but differ in being bifurcated, and in the shedding of their sheath. Remains of *Antilocapra* occur in the Pleistocene of North America; and it is thought that *Cosoryx*, of the Pliocene of the same country, may have been the direct ancestor of the existing genus.

Family Bovidæ.—In this, the last, family are comprised the most specialised members of the whole suborder, such as the Antelopes, Goats, Sheep, and Oxen. The general characters of the greater part of the skeleton are the same as those mentioned under the head of the *Cervidæ;* but a remarkable difference is found in respect of the frontal appendages. These appendages (fig. 1222) are paired, and consist of persistent bony processes, into which the air-cells from the frontal diplöe often extend; they are generally subconical or triangular, and often twisted, but never branched. These "horn-cores," as they are termed, are covered with the true horns, which are composed of an epidermal fibrous structure, and are never shed. The males of all existing genera in the wild state are furnished with these horns, and they are also present, although of smaller size, in the females of the great majority. In certain domesticated races of so-called *polled* Sheep (fig. 1220), Goats, and Cattle, the horns are, however, wanting in both sexes; and this peculiarity is with great probability regarded as an instance of reversion, since these appendages are also wanting in some allied Tertiary forms of two of these groups. In the cranium there is generally no lachrymal vacuity, and the lachrymal

consequently articulates largely with the nasal (fig. 1220); but in certain Antelopes this vacuity is present, when the relations of these bones are the same as in the *Cervidæ*. Another very characteristic feature of the *Bovidæ*, as a whole, is the hypsodont character of their cheek-dentition. In many of the Antelopes (fig. 1221) this feature is only moderately developed, but in the Sheep, Goats, and Oxen it is carried to an excessive degree; and in the latter group the valleys of the teeth are filled up by a coating of cement. This feature, like that of the relations of the lachrymal, is, however, not absolutely distinctive of the *Bovidæ*, since we find many Antelopes

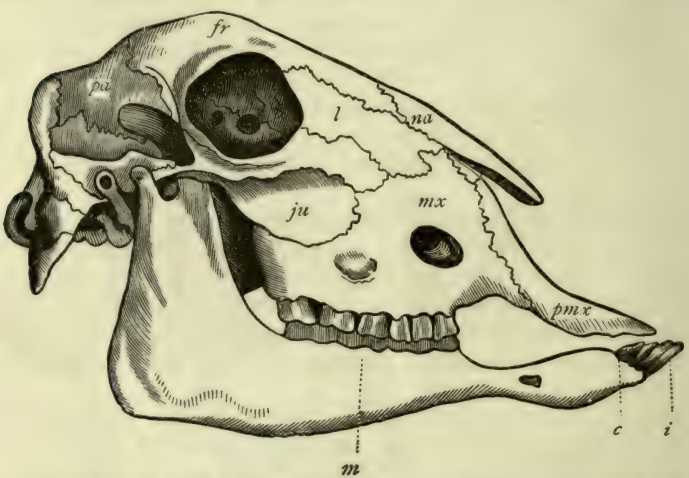


Fig. 1220.—Skull of a hornless Sheep (*Ovis*). Reduced. *i*, Incisors; *c*, Canines; *m*, Cheek-teeth; *pmx*, Premaxilla; *mx*, Maxilla; *na*, Nasal; *l*, Lachrymal; *ju*, Jugal; *fr*, Frontal; *pa*, Parietal. (After Owen.)

(and especially those having a lachrymal vacuity) with a decidedly brachydont dentition. The upper true molars frequently have a large accessory inner column (fig. 1221). Functional canines are wanting in all existing forms. The lateral digits may or may not be present, but in no living form is there a distal remnant of the lateral metapodials.

This family does not apparently date further back than the Middle Miocene, where it is represented by members of its least specialised group, the Antelopes; the Sheep and Oxen not appearing till the Pliocene. It has been suggested that the family originated from the same ancestral forms as the *Cervidæ*.

Commencing with the Antelopes, and confining our attention to those forms in which the genus has been more or less accurately determined, we find in the *Alcelaphine* section, which is now con-

fined to Africa and Syria, the existing genus *Alcelaphus* represented in the later Tertiaries of Algeria, and also in the Pliocene Siwaliks of India; the species from the latter deposits being apparently allied both to the Hartebeast (*A. caama*) and the Bontebock (*A. pygargus*). These antelopes have recurved or lyre-shaped horns; their skull has no supraorbital pits, and may have a very long face; while the molar teeth are very narrow. In the *Cephalopine* section, comprising Indian and African species of comparatively small size, the existing Four-horned Antelope (*Tetraceros quadricornis*) is found in a fossil state in the cave-deposits of Madras;

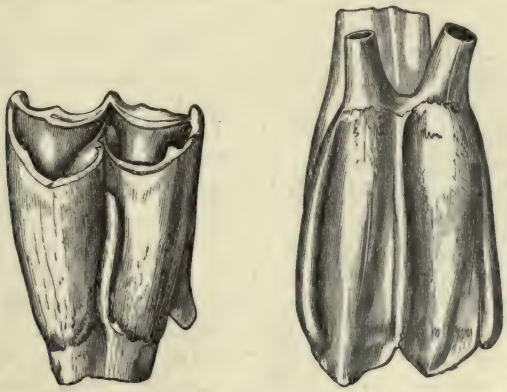


Fig. 1221.—Inner and outer views of the second left upper true molar of the Nilghai (*Boselaphus tragocamelus*). Recent; India.

while an extinct species occurs in the Siwaliks. The African genus *Cephalopus* may perhaps also occur in the latter deposits. The *Cervicaprine* section is now confined to Africa, and includes some very large antelopes in which the females are hornless. *Cobus*, in which the skull has well-marked supraorbital pits, appears to be represented in the Indian Siwaliks by species as large as some of the African forms. In the Pliocene Pikermi beds of Greece an antelope with round lyrate horns, described as *Helicophora*,[1] appears to be allied in some respects with *Cobus*, although it has lachrymal vacuities, but no distinct supraorbital pits. In the typical *Antelopine* section, which is allied in many respects to the preceding, there are always well-developed supraorbital pits, and the molar teeth are hypsodont, and resemble those of the sheep. The type genus *Antilope*, which has round and spirally twisted horns, is known in the Pleistocene of India by remains of the one existing species *A. cervicapra* (Black-buck); the existing Siberian *Saiga tartarica* is

[1] Originally described under the preoccupied name of *Helicoceros*.

found fossil in the cave-deposits of Europe; while the Afro-Asiatic genus *Gazella*, in which the lyrate horns are laterally compressed, occurs in the Pliocene of Europe, Africa, and India, as well as in the Norfolk Forest-bed. The *Hippotragine* section may be taken to include the existing African genera *Oryx*, *Addax*, and *Hippotragus*, and is characterised by the long and straight, or backwardly-curved horns, the absence of supraorbital pits in the skull, and the broad and hypsodont upper molars, which resemble those of the oxen. In a fossil state this section is represented by *Hippotragus* in the Indian Siwaliks; and also by the extinct *Palæoryx*, of the older Pliocene of Greece, Italy, Samos, and France, which appears to have been closely allied to *Oryx*, although showing some affinity to *Hippotragus*. The last section into which the true existing antelopes may be divided is the *Tragelaphine*, comprising *Boselaphus* in India, and *Tragelaphus*, *Strepsiceros*, and *Oreas* in Africa. In the Indian genus, of which the Nilghai is the only existing representative, the horns are short and upright, and are not present in the females, while the dentition is hypsodont (fig. 1221); fossil forms occur in India from the Siwaliks upwards. In the African forms the horns are spirally twisted, with two more or less well-defined longitudinal ridges, the skull has deep supraorbital pits and lachrymal vacuities, but no pit in the lachrymal itself, and the molars are broad and brachydont like those of the *Cervidæ*. *Strepsiceros* (Kudu), in which the anterior ridge on the horns is much the stronger of the two, apparently occurs in the Indian Siwaliks, which may also contain a representative of the allied *Oreas* (Eland). The extinct *Palæoreas* (fig. 1222), of the Lower Pliocene of Europe and Algeria, appears to have been allied to both the preceding genera; while the so-called *Antilope torticornis*, of the Pliocene of France, has the posterior ridge of the horns the most developed, as in the existing *Tragelaphus*, to which genus it has, indeed, been referred. The remarkable *Protragelaphus*, of the Lower Pliocene of Greece, differs from all the preceding genera in that the horns have only a posterior longitudinal ridge, in the absence of supraorbital pits, and in the development of lachrymal depressions like those of the *Cervidæ*. With the *Rupicaprine* section of this family we come to genera showing characters connecting the true antelopes with the goats; but the only definitely known fossil remains belong to the existing alpine Chamois (*Rupicapra*), which occurs fossil in the cave-deposits of the Continent. Under the name of the *Palæotragine* section may be included three extinct Tertiary genera having the laterally compressed horn-cores of the goats, but the upper molars more or less like those of the brachydont antelopes. The earliest of these genera, and indeed of all the antelopes, is *Protragoceros*, of the Middle Miocene of France, one of the species having been long

since described as *Antilope clavata* (*sansaniensis*). These were small forms, with short horns, and the crowns of the molars very short and moderately wide. In *Palæotragus* and *Tragoceros*, of the Lower Pliocene of Greece and Samos, the horns were larger, and the molars wider. The former genus is considered to be allied to *Samotherium*, noticed among the *Giraffidæ*. The true Goats and Sheep, collectively forming the section *Caprinæ*, are characterised by their more or less laterally compressed and often angulated horn-cores, which may be either curved backwards, as in the Ibex, spirally twisted, as in the Markhoor, or with a peculiar outward curvature and twist, as in the Sheep; the horns themselves being frequently

Fig. 1222.—Left lateral view of the cranium of *Palæoreas Lindermayeri;* from the Lower Pliocene Pikermi beds of Greece. Reduced. The lachrymal vacuity is omitted. (After Gaudry.)

marked on the anterior surface by transverse ridges. In all the genera the dentition is markedly hypsodont, and in existing forms the accessory inner column of the upper true molars is wanting. None of them show a lachrymal vacuity; but in the Sheep there is generally a deep depression (larmier) in this bone, which is absent in the Goats. *Capra* may perhaps occur in the Upper Pliocene of France; it is represented in the Pliocene of the Indian Siwaliks by one species (*C. sivalensis*), which is probably the ancestor of the Himalayan Thar (*C. jemlaica*); by another species equally closely allied to the Markhoor (*C. Falconeri*), of the same region; and not

improbably by a third allied to the Himalayan Ibex (*C. sibirica*). Remains of the Pyrenean Ibex (*C. pyrenaica*) are found in the Pleistocene cave-deposits of Gibraltar; and those of the common Goat (*C. hircus*) in the turbaries and fens of England. The very remarkable hornless genus *Bucapra*, from the Siwaliks of India, has a skull presenting a great resemblance to that of the Goats, but cheek-teeth like those of the Oxen. The true Sheep (*Ovis*) appear to be a group of very late origin, and are scarcely known in a fossil condition; a large species has, however, been described from the Norfolk Forest-bed as *O.* (*Caprovis*) *Savigni*, which was apparently allied to the existing Argali. The Musk-Ox (*Ovibos*) of the Arctic regions, which forms a connecting link between the *Caprinæ* and *Bovinæ*, occurs fossil in the Pleistocene of Europe and Alaska; while two closely allied forms, from the Pleistocene of Kentucky and Arkansas, have been respectively named *O.* (*Boötherium*) *bombifrons* and *O. cavifrons*.

The members of the *Bovine* section, comprising about thirteen recent species distributed over the greater part of Europe, Asia, Africa, and North America, agree with the *Caprine* section in having no lachrymal vacuities, but differ from the recent members of that section in having the crowns of the cheek-teeth extremely tall, with large accessory columns in the upper true molars, and their valleys filled up by a large quantity of cement. The horn-cores may be either rounded, flattened, or angulated, and are frequently directed more or less outwardly, but are never curved spirally inwards, or of the "cork-screw" shape characteristic of many Goats; while the horns themselves are not marked on their anterior surface by prominent transverse ridges. The most aberrant genus is *Leptobos* from the Pliocene and Pleistocene of India and the Upper Pliocene of Italy, in which the frontal portion is broad, with widely separated horn-cores placed far below the level of the occiput. The horn-cores are sometimes absent; and this genus is regarded as allied to *Boselaphus*. *Bubalus*, typically represented by the Buffaloes of India and Africa, but which may also be taken to include the diminutive Anoa (*B. depressicornis*) of Celebes, is characterised by its angulated horn-cores, which may be directed either outwards or upwards, and by the great convexity of the forehead in the more typical forms. Among the more aberrant species may be reckoned three from the Siwalik Hills of India (*e.g.*, *B. occipitalis*), which are closely allied to the Anoa, and (together with that species) by some writers are termed *Probubalus;* the horn-cores are frequently completely triangular in section, and the forehead is not decidedly convex. *B. platyceros* from the same deposits is intermediate between the last-mentioned group and the existing Buffaloes. *B. antiquus* from the Pleistocene of Algeria is regarded by Professor Rütimeyer as closely

allied to the existing African Buffaloes, although Dr P. Thomas thinks it is more nearly related to the living Indian species. The latter (*B. buffelus*) is found in a fossil state in the Pleistocene of the Narbada Valley, India; while an apparently closely allied form also occurs in the Pliocene of the Siwalik Hills. In *Bison*, now represented by the Aurochs of Lithuania (*B. bonasus*) and the nearly exterminated North American *Bison americanus*, the skull is characterised by its great relative width and shortness, the tubular orbits, the moderately convex forehead, and the curved, round, horn-cores, which are placed considerably below the level of the occiput. The existing European species is represented by a variety (*priscus*) in the Pleistocene of Europe and Arctic America; while the gigantic *B. latifrons* of the Pleistocene of Texas may probably be looked upon as the progenitor of the recent species of that country. A cranium from the Pliocene of the Siwalik Hills has been referred to this genus with the name of *B. sivalensis*, and appears to be allied to existing forms. The genus *Bos*, which is confined to the Old World, is the most specialised representative of this section, and may be divided into the *Bibovine* and *Taurine* groups. In the former are included the wild Oxen of India and Burma, which are characterised by

Fig. 1223.—Cranium of the Urus, *Bos taurus*, var. *primigenius*, Pleistocene. Much reduced.

the more or less flattened horn-cores, and by certain peculiarities in the form of the occipital region. The earliest representative of this group is *Bos etruscus* from the Upper Pliocene of the Continent, in which the horn-cores are placed very low down on the frontals; this species being considered to be nearly related to *B. banting* of Burma. A more imperfectly known member of this group is *B. palæogaurus* of the Pleistocene of India, which may turn out to be identical with

B. gaurus now living in the same regions. In the *Taurine* group the frontals (fig. 1223) are extremely elongated, and the horn-cores, which in the type species are rounded, are placed immediately over the occiput. To this group may be referred *B. planifrons* and *B. acutifrons* of the Pliocene of the Siwalik Hills; the latter being remarkable for its sharply angulated frontals and its enormous horn-cores, which have a pyriform section. Another member is *B. namadicus* of the Pleistocene of Central India, which presents some approximation to the *Bibovine* group; but the best known fossil Ox is the Urus of the European Pleistocene (fig. 1223), which appears to be only a larger form of the existing Ox (*Bos taurus*), and of which the descendants of wild races are still preserved in Chillingham and some other British parks. A still smaller race, whose remains have been found in the turbaries and fens of England, and have been described under the names of *B. longifrons* and *B. frontosus*, seems to be only a stunted variety of the same species, from which it is probable that the small cattle of Wales and Scotland have been derived.

Suborder 2.—Perissodactyla.—The characters possessed by this suborder in common with the Artiodactyla are noticed under that head. The distinctive features of the Perissodactyla are to be found in the truncated distal surface of the astragalus (fig. 1224); the circumstance that the third digit in both the fore and hind feet is symmetrical in itself, and larger than either of the others (fig. 1225); the presence (except in *Chalicotherium*) of a third trochanter to the femur (fig. 1226); and the non-articulation of the fibula with the calcaneum. Other characters very generally observable in this suborder are, that the whole of the series of cheek-teeth are in contact with one another; that the upper premolars are nearly or quite as complex as the true molars; that the last lower true molar frequently has no third lobe, and that when such third lobe is present, it is absent in the last lower milk-molar; while the first tooth of the cheek series is sometimes preceded by a milk-tooth. In all existing forms the number of the dorso-lumbar vertebræ is never less than twenty-two, and is usually twenty-three; while the nasals are expanded posteriorly. The stomach is simple, and the placenta diffused. In existing forms the cervical vertebræ are markedly opisthocœlous. The upper true molars are constructed on some modification of what is known as

Fig. 1224.—Anterior view of the left astragalus of the Horse (*Equus caballus*). One-half natural size.

the *Lophodont* plan (fig. 1228); that is, there is an outer longitudinal wall, from which two transverse ridges proceed at right angles towards the inner border of the crown. In the brachydont forms this structure is perfectly simple, but in those genera with very hypsodont teeth it is so complicated by foldings and involutions that it is not always easy to trace the original plan. The crowns of the lower true molars consist in their simplest structure of two transverse ridges (as in the Tapir), but these ridges may be curved into crescents (as in the Rhinoceros), or complicated by foldings

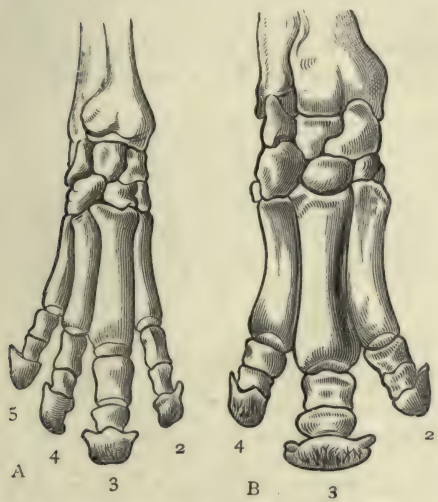


Fig. 1225.—Right manus of (A) *Tapirus*, and (B) *Rhinoceros*. Reduced. (After Flower.)

Fig. 1226.—Dorsal or anterior view of the left femur of *Rhinoceros*. The median projection on the right side of the figure is the third trochanter. Reduced.

and convolutions (as in the Horse). The transition from the simplest brachydont to the most specialised hypsodont dentition is accompanied by a reduction of the number of the digits from four or three to one; that one being the third, or middle, of the typical series of five.

The Perissodactyla have suffered considerably more in proportion to their numbers than the Artiodactyla by the extinction of generic and family types; the existing genera being at the present day reduced to three, which are the types of as many different families. Some writers have suggested that this extinction of types is owing to the Lophodont plan of molar structure being less readily suscep-

tible of modification than the Bunodont type upon which the Artiodactylate molar is constructed, but this is really a pure assumption.

Family Tapiridæ.—This family is represented by the single existing genus *Tapirus*, now found in the widely separated areas of the Malay Peninsula and South America, and thus affording an excellent example of what is termed discontinuous distribution. The dental formula is $I.\ \frac{3}{3},\ C.\ \frac{1}{1},\ Pm.\ \frac{4}{3},\ M.\ \frac{3}{3}$; the cheek-teeth are brachydont, and of the simple Lophodont type; the hinder premolars being as complex as the true molars, and the last lower molar having no third lobe. The first upper premolar has a deciduous predecessor; and in the existing forms there are four digits in the anterior (fig. 1225, A), and three in the hind foot. The cranium (fig. 1227) has its cerebral portion much vaulted, and the

Fig. 1227.—Side view of the skull of *Tapirus americanus*. Reduced. (After Giebel.)

nasals short and arched; in one American species (which on this account is regarded by some authors as generically distinct under the name of *Elasmognathus*) the narial septum is largely ossified; and there is a short proboscis. In Europe this genus is found in the Middle Miocene of France (*T. Poirrieri*), and continues to the Upper Pliocene (*T. arvernensis*); it also occurs in the Pliocene of China (*T. sinensis*), and in the Pleistocene cave-deposits of Brazil, one of the forms from the latter being indistinguishable from the living *T. americanus*. The North American Miocene forms named *Tapiravus* are probably not generically distinct. An imperfectly known form from the Middle Eocene of France, described as *Palæotapirus*, is referred by Dr Filhol to this family.

Family Lophiodontidæ.—This Eocene family presents characters allying it very closely with the *Tapiridæ*, *Palæotheriidæ*, and *Rhinocerotidæ*, and probably contains ancestral forms of all those families. The upper true molars (fig. 1228) are brachydont, and always more complex than the premolars; the last lower true molar

generally has a third lobe; and there are usually four digits in the manus and three in the pes. The type genus *Lophiodon* (fig. 1228, A) comprises some species which attain a bulk rivalling that of the Rhinoceroses, and has the dental formula $I.\frac{3}{3}, C.\frac{1}{1}, Pm.\frac{3}{3}, M.\frac{3}{3}$. It is found in the Middle and Upper Eocene of Europe, and is generally regarded as having died out without descendants. In the dentition here figured the inner crescent of the fourth upper premolar is incomplete, and the ridges of the lower molars are simple; the last lower true molar always has a third lobe. Allied to *Lophiodon* is *Helaletes* (*Desmatotherium*), of the Upper Eocene of North America, characterised by the more rounded upper true molars and the absence of a diastema in the lower jaw; it is re-

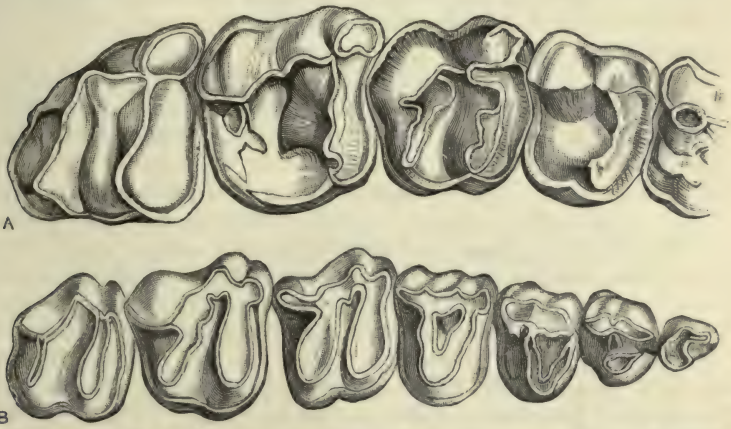


Fig. 1228.—A, The last five right upper cheek-teeth of *Lophiodon isselensis*, from the Middle Eocene of France; B, The right upper cheek-teeth of *Hyrachyus agrarius*, from the Eocene of North America. Reduced.

garded by Professor Cope as an ancestral stock of the *Rhinocerotidæ*. With forms from the North American Eocene described as *Isectolophus* and *Prothyracodon*, in the first of which the last lower true molar has a third lobe, we come to the consideration of Lophiodonts showing more affinity with the Tapirs, but it does not appear quite certain that both these forms are really entitled to generic distinction from the next. The genus *Hyrachyus* (fig. 1228, B), which occurs typically in the Uinta and Bridger Eocene of the United States, is taken by Dr Filhol to include European Lophiodonts ranging from the Middle Eocene of France to the Lower Miocene of St Gérand-le-Puy. This genus has four premolars, of which the last is somewhat simpler than the first true molar; while there is no third lobe to the last lower true molar. In the type species the

upper true molars (fig. 1228, B) resemble those of the *Rhinocerotidæ;* but there appears to be a gradual transition in this respect towards *H. priscus*, of the Quercy Phosphorites, in which these teeth have rounded angles, and approximate to those of the Tapirs; from which, however, these forms are distinguished by the simpler fourth premolar. This transition has induced Dr Filhol to abolish the genus *Protapirus*, which was proposed for *H. priscus*. The latter species is evidently allied to the American *Isectolophus;* and Dr Filhol suggests a transition from this type towards the Tapirs. The typical American species of *Hyrachyus* is regarded as the ancestor of the genus *Hyracodon*, which is classed in the *Rhinocerotidæ*. An American species which may be provisionally included in *Hyrachyus* is said to have an attachment for a dermal horn on each nasal, on which account it is separated by Professor Marsh as *Colonoceros*. The American Eocene genus *Dilophodon* appears to be allied to this group.

The imperfectly known genus *Ribodon*, from the infra-Pampean beds of Patagonia, is apparently nearly allied to *Hyrachyus*. The genus *Triplopus*, of the Upper Eocene of the United States, is distinguished by having only three digits in the manus, on which account Professor Cope makes it the type of the family *Triplopodidæ*. In *Hyracotherium*, with which the forms described under the names of *Pliolophus* and *Orohippus*, and not improbably *Eohippus*, are identical, the upper true molars resemble those of *Lophiodon*, but their anterior ridge is incomplete, and the transverse ridges of the lower cheek-teeth have a tendency to assume a crescent-shape. In this genus there is a diastema behind the first premolar, but in an allied form from the Lower Eocene of North America, which has been named *Systemodon*, all the teeth are in contact. The numerous species of *Hyracotherium* indicate animals not larger than a Fox; the dentition is of the full typical number, and the structure of the fore-foot is shown in fig. 1236, A. This genus occurs in the Lower Eocene[1] both of Europe and North America, and, as will be more fully noticed below, it is regarded as the ancestral stock of the *Equidæ*. *Heptodon*, from the Eocene of New Mexico, which was originally identified with *Pachynolophus*, appears to connect the latter with *Hyracotherium*, although it is placed by Professor Cope next to *Hyrachyus*. In *Pachynolophus* the dental formula is of the full typical number; but the upper true molars have taller ridges than in *Hyracotherium*, and are intermediate in structure between those of the latter and of *Anchilophus;* the lower molars being subcrescentoid. The largest species is *P. isselanus*, but there are

[1] It has recently been recorded from the Middle Eocene and the Phosphorites of France; but at least one of the species from the latter deposits indicates a form more nearly allied to *Anchilophus*.

several other forms from the Middle and Upper Eocene of the Continent; *Propalæotherium* (in which *Lophiotherium* may be included) does not appear generically separable.

Family Palæotheriidæ.—With the *Palæotheriidæ* we enter upon another extinct family of this suborder, the type genus of which has long been known from the classic labours of Cuvier. In this family the upper premolars may be either simpler or quite as complex as the true molars; the lower molars have crescentoid crowns, and in the last tooth of this series the third lobe may be either well developed or almost wanting; all the cheek-teeth are brachydont, and when cement is present it does not fill their valleys. There are always three digits in each foot. The type genus *Palæotherium*, in which may be included *Paloplotherium* (or *Plagiolophus*), ranges from the Middle Eocene of the Paris basin to the Lower Miocene of Ronzon, but is especially characteristic of the Parisian stage. The dental formula is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{(3-4)}{(3-4)}$, $M.\frac{3}{3}$; and the last lower molar has a third lobe. In the more typical species (fig. 1229) the four premolars are present in both jaws, the fourth upper pre-

Fig. 1229.—The right upper cheek-dentition of *Palæotherium crassum*; from the Upper Eocene of Paris. Reduced.

molar is as complex as the first true molar, and the third lower premolar as the fourth lower premolar; while the diastema is comparatively short, and the canines are not large. The upper true molars of all the species exhibit an expansion of the inner extremities of the transverse ridges, foreshadowing the structure of the teeth of some of the *Equidæ*. The cranium is Tapiroid in character, especially in the prominence of the nasal bones; from which it is deduced with great probability that the nose possessed a short movable proboscis. The general form may also be supposed to have been like that of the Tapirs, and the restoration of *P. magnum* given by Cuvier (fig. 1230) exhibits to us an animal closely similar to the existing Tapir. In this particular instance, however, we know that the restoration is incorrect, since the discovery of a complete skeleton of this species has shown that it was a more slender and longer-necked animal, resembling in its general figure a Llama.

In that group, which is considered by some writers as generically distinct under the name of *Paloplotherium*, the last upper premolar has its

hinder lobe more or less completely aborted, the third lower premolar is less complex than the fourth, the first lower premolar is absent, and the corresponding upper tooth may also be wanting; when the latter tooth is present it is sometimes preceded by a milk-molar. In this group *P. Javali*, from the Quercy Phosphorites, is remarkable for the presence of a considerable quantity of cement in the cheek-teeth, and for the approximation of the upper canine to the premolars and its apparent separation from the incisors. *P. minus* from the Paris basin is the smallest species

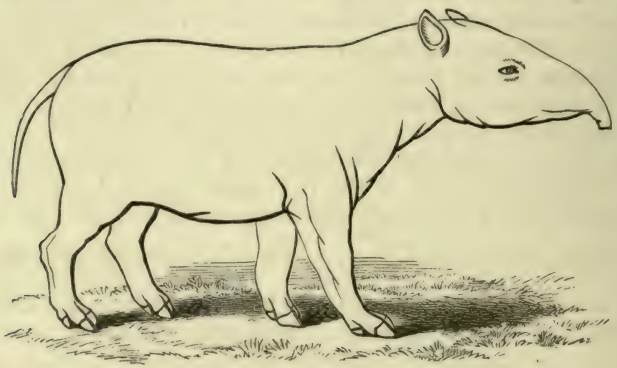


Fig. 1230.—Reduced restoration of *Palæotherium magnum*, after Cuvier. Upper Eocene, France.

of the genus; while *P. codiciense*, from the Middle Eocene of France, has its fourth upper premolar as simple as in *Lophiodon* and *Hyrachyus*, and thus shows how extremely intimate is the relation between all these early forms of the suborder, and how very difficult it is to give any good distinctive characters of the families into which it is convenient to divide them.

In *Anchilophus*, of the Upper Eocene of the Continent, the dental formula is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{?4}{3}$, $M.\frac{3}{3}$; and the cheek-teeth are nearly intermediate in structure between those of *Pachynolophus* and *Anchitherium*. The last upper premolar is as complex as the first true molar; there are well-marked ridges on the outer columns of the upper true molars; the last lower true molar has a large third lobe; and the diastema is elongated. The genus *Epihippus* from the Upper Eocene of North America, which is reckoned by some writers as being on the direct ancestry of the Horse, has been placed here by Dr Schlosser. The genus forming a step in advance of *Anchilophus* is *Anchitherium*, typically from the Middle Miocene of Europe, but with which the contemporary North American forms described under the names of *Mesohippus*

Fig. 1231. — A left upper true molar of *Anchitherium aurelianense*; from the Middle Miocene of France.

and *Miohippus* may be united. The dental formula is the typical one; the upper premolars are as complex as the true molars (fig. 1231), the external surface being without a median vertical ridge; the first lower premolar is comparatively small; and the third lobe of the last lower true molar is reduced to a small talon; while the incisors have no infolding of the enamel at their summits. Some species show a "larmial" depression in the lachrymal. The typical *A. aurelianense* (fig. 1231), of the Middle Miocene of the Continent, is the largest species, and shows no trace of the fifth metacarpal; while the meso- and entocuneiform of the tarsus are united. In the smaller *A. Bairdi* of the Miocene of North America the lateral digits are relatively larger, the fifth metacarpal is represented by a splint, and the meso- and entocuneiform are separate. Allied to this genus are *Anchippus*, *Parahippus*, and *Hyohippus* of the North American Miocene.

Fig. 1232.—Lateral view of the right manus of the Horse (*Equus caballus*). Reduced. *ca*, Carpus; *m*, 3d Metacarpal (cannon-bone); *s*, Lateral do.; 1, 2, 3, Phalangeals of third digit.

FAMILY PROTEROTHERIIDÆ.—In this place it may be convenient to notice the genus *Proterotherium* from the Tertiary of Patagonia, which was at first regarded by Dr Ameghino as belonging to the Artiodactyla, but was subsequently made the type of a distinct family of this suborder. One species was referred by Bravard to *Anoplotherium*, while a second was subsequently described by Dr Burmeister first as *Anchitherium*, and then as *Anisolophus*. The upper premolars are nearly as complex as the true molars. The names *Thoatherium*, *Diadophorus*, and *Licaphrium* have been applied to allied forms from the same deposits. The lower molars have four distinct roots. It may be questioned whether these forms are really entitled to form a distinct family.

FAMILY EQUIDÆ.—The division between this family and the *Palæotheriidæ* is a more or less arbitrary one. In the present one the upper premolars are as complex as the true molars, and all the cheek-teeth are usually of an extremely hypsodont type, with their valleys filled with cement; the crowns of the lower molars are crescentoid, with complex folds of enamel, and there is scarcely any distinct third lobe to the last lower molar. The digits may be

either one (fig. 1232) or three in number; the ulna and fibula are incomplete; and the meso- and entocuneiform of the tarsus are united. The plane of wear of the cheek-teeth becomes nearly smooth, instead of being raised into ridges as in the preceding families; and the summits of the incisors have an infolding of the enamel extending some distance into the crown. One of the most generalised forms is *Protohippus* or *Merychippus* of the Lower Pliocene of North America, in which the permanent molars resemble those of the generalised species of *Equus*, but have shorter crowns, while the milk-molars approximate more nearly to the true molars of *Anchitherium*. The next genus is *Hipparion* (*Hippotherium*). The dentition is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{4}{3}$, $M.\frac{3}{3}$; but the first upper cheek-tooth, which has no predecessor and appears with the milk series, is shed before the animal is adult. The upper cheek-teeth (fig. 1233) at first sight seem to differ very widely

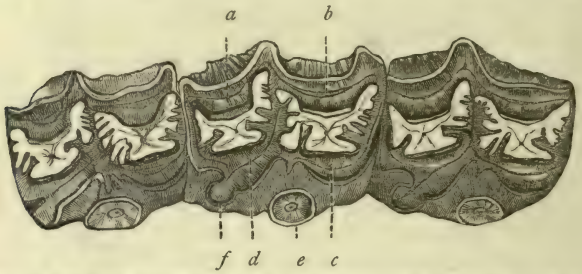


Fig. 1233.—Three right upper cheek-teeth of *Hipparion*; from the Pliocene of India. *a*, Posterior, and *b*, Anterior outer crescent; *c*, Anterior, and *d*, Anterior inner crescent; *e*, Anterior, and *f*, Posterior pillar.

from those of the *Palæotherium* type (fig. 1229), but a closer examination will show that the outer portions marked *a* and *b* correspond to the outer wall of the more generalised tooth; while the portions *c* and *e*, and *d* and *f* respectively represent the first and second transverse ridges of the same. These ridges have, however, united together in a crescent-like form, and enclose between them and the outer wall a pair of islands surrounded by a plicated wall of enamel and filled with cement. The terms which it is convenient to apply to the Equine molar are indicated in the accompanying figure; and the distinctive feature of the upper teeth of *Hipparion* is that the anterior pillar (*e*) is disconnected from the anterior inner crescent (*c*) for at least three-quarters of its height, so that it normally appears on the worn crown as an isolated oval (fig. 1233). There are normally three digits to each foot, but in the Pliocene Indian *H. antilopinum* they are apparently reduced to one; this

form having been made the type of the genus *Hippodactylus*. The best known species is *H. gracile* of the Pliocene of Europe, Samos, Persia, and Algeria; but the genus is also well represented in the Pliocene of India (*H. antilopinum*, *H. Theobaldi*), China (*H. Richthofeni*), and North America. All the species retain the primitive feature of a depression in the lachrymal. With *Equus* (in which may be included the American *Hippidium*, otherwise *Pliohippus*) we come to the most specialised of all the Perissodactyla. The dentition is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{(3-4)}{(3-4)}$, $M.\frac{3}{3}$; but the first upper cheek-tooth is usually absent in existing forms, and the corresponding lower one is only occasionally developed in some extinct species. The crowns of the cheek-teeth are higher than in *Hipparion*, and the anterior inner pillar of the upper ones, except in a very early stage of wear, is connected with the adjacent inner crescent (fig. 1234). There is but one functional digit to each foot, although the

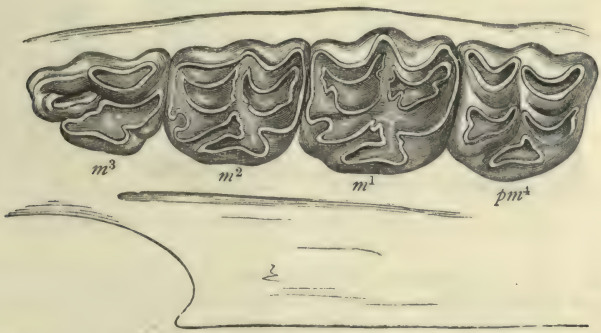


Fig. 1234.—The last four right upper cheek-teeth of the Horse (*Equus caballus*). Reduced.

proximal portions of the lateral metapodials remain (figs. 1232, 1236, D), and in the so-called *Hippidium* the terminal phalangeals were represented by claws. A maxillo-lachrymal fossa is present in the extinct *E. andium* and *E. sivalensis*, but is wanting in all existing species. At the present day this genus is confined to the Old World, and is especially characteristic of Africa, but in the Pliocene and Pleistocene it was spread over both North and South America.

In those South American Pleistocene forms referred by some writers to *Hippidium*, the molars are shorter and more curved than in existing species, and the grinding surface of the anterior pillar of the upper ones is not wider than in *Hipparion; E. principalis* is a large species of this type. In *E. Stenonis* of the Upper Pliocene of Italy, Kos, and Algeria, and the Norfolk Forest-bed, the molars are taller, but they still

have a narrow anterior pillar in the upper jaw, and thus show their connection with *Hipparion*. In *E. sivalensis*, of the Pliocene of India, and *E. quaggoides* of that of Italy, this pillar becomes rather more widened; and in the Pleistocene *E. namadicus* of India, as well as in *E. curvidens* of that of Brazil, and all the existing members of the genus (fig. 1234) the grinding surface of this pillar becomes greatly widened in the antero-posterior direction. It is noteworthy that *E. sivalensis* is found in the same beds as those containing *Hipparion;* and that the existing *E. caballus* is apparently the common species of the European Pleistocene, although it is not improbable that the Asiatic *E. onager* may also occur in the same deposits. In Southern India, where no living species are found, the remains of the existing African *E. asinus* and of a larger

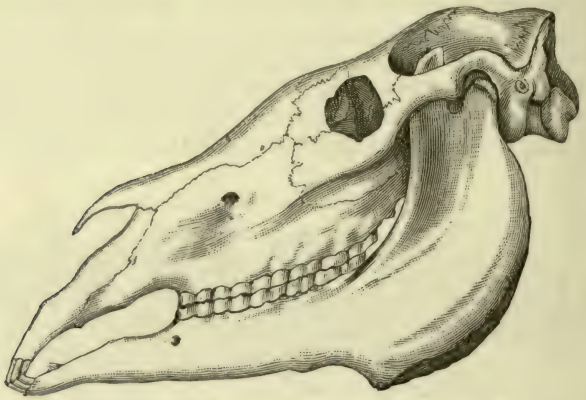


Fig. 1235.—Skull of the Horse (*Equus caballus*). Reduced.

undetermined form occur in the Pleistocene cave-deposits of Madras. Finally, it should be mentioned that some of the South American Tertiary forms have been separated under the name of *Haplohippus*.

GENEALOGY OF THE HORSE.—Allusion has been incidentally made in the preceding paragraphs to the genealogy of the genus *Equus*, but since this is one of the best instances of evolution among the higher Mammals yet worked out it is advisable that it should be noticed rather more fully. The top of the series is the *Equus caballus* group, in which the dentition is of the most specialised type, and which descends in India to the topmost Pliocene; then we have the *E. Stenonis* and *E. principalis* group, in which the molars become more like those of *Hipparion;* and finally the so-called *Hippidium*. The structure of the foot is shown in fig. 1236, D; the great size of the phalangeals and the metapodial of the functional digit being very noticeable. The earliest occurrence of the genus is in the Pliocene of India. From the *E. Stenonis* group to *Hipparion* is but a step, the transitional species being *H. antilopinum* of the Pliocene of the Siwalik Hills in which the lateral digits were apparently wanting; in the other species (fig. 1236, C) the lateral digits are of small size, and the middle one is relatively more slender than in *Equus*. *Protohippus* connects *Equus* by the structure of its milk-molars with the Miocene *Anchitherium:* and in the latter the teeth have become brachydont, the third lower molar has a small third lobe, and the lateral

digits of the foot (fig. 1236, B) have become larger and the middle digit smaller; traces of the fifth metacarpal being retained in the American species. The next step is probably made by some form allied to *Anchilophus* or *Pachynolophus* of the Upper Eocene; and from such a type the transition is easy to the Lower Eocene *Hyracotherium* and *Systemodon*, in which all the species are very small, the dentition is of the simple Lophodont type, with a large third lobe to the last lower true molar, and the fore-foot (fig. 1236, A) has four complete digits, which are of subequal size; while there may be (*Eohippus*) a rudimental metacarpal of the pollex. Finally, the earliest stage of this series is formed by *Phenacodus* of the Lowest or Puerco Eocene of North America, in which there are five digits to each foot, and of which the structure will be more fully noticed under the head of the suborder Condylarthra. It should be observed, however, that Professor Cope would introduce an inter-

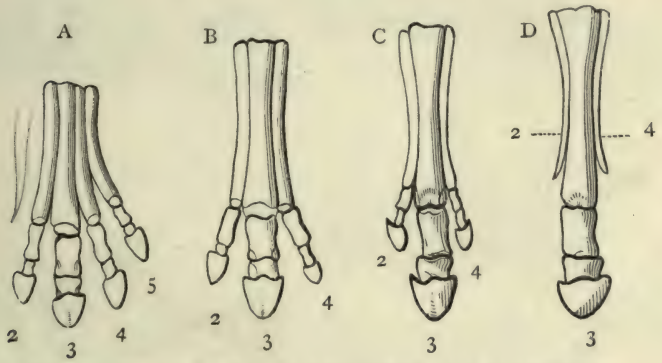


Fig. 1236.—Bones of the left manus of *Hyracotherium* (A), *Anchitherium* (B), *Hipparion* (C), and *Equus* (D).

mediate stage between *Systemodon* and *Phenacodus;* and that the same authority also introduces the genus *Palæotherium* between *Hyracotherium* and *Anchitherium*, although most writers regard that genus as quite off the line.

In this connection may be noticed the remarkable circumstance that in the line of evolution culminating in the modern Horse a parallel series of generically identical or closely allied forms occurs in the Tertiaries of both Europe and North America, from which it has been suggested that in both Continents a parallel development of the same genera has simultaneously taken place—*i.e.*, that in both regions *Anchitherium* has given rise to *Hipparion*, and *Hipparion* or an allied type to *Equus*. Now, seeing it is evident that in the case of species of a single genus the evolution has taken place in separate lines,—that is to say, that the existing Indian species of *Canis* are probably derived directly from the Pliocene forms of the same region, and the Brazilian species of that genus have their predecessors of the cave-epoch of that country,—there appears no logical reason for refusing to admit an analogous parallel evolution in the case of genera, and there is accordingly a considerable probability that the hypothesis in question may be a true one. Professor Cope considers that in one country *Protohippus*, and in the other *Hipparion*, was the immediate ancestor of *Equus*.

Family Rhinocerotidæ.—With this family we enter upon the consideration of another branch probably derived from the primitive Lophiodont stock, which attained great development in Tertiary times, and is still represented in Asia and Africa by at least five well-defined species. It is not easy to distinguish this family from the *Lophiodontidæ*, as represented by *Hyrachyus* (which Dr

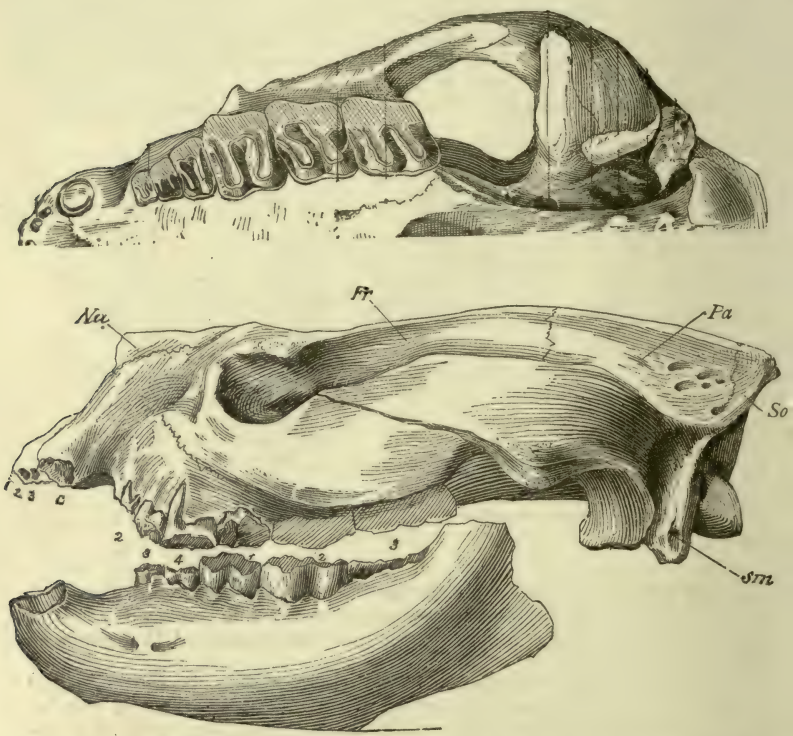


Fig. 1237.—Left half of the palatal surface of the cranium, and left lateral aspect of the skull of *Metamynodon planifrons;* from the White River Miocene of North America. One-sixth natural size. *Na*, Nasal; *Fr*, Frontal; *Pa*, Parietal; *So*, Supraoccipital; *sm*, United postglenoid and posttympanic processes; 1, 2, 3, Alveoli of incisors; *c*, Alveolus of canine; 2, 3, 4, Premolars; 1, 2, 3, True molars. (After Scott and Osborn.)

Schlosser includes in the *Rhinocerotidæ*), but the upper true molars (fig. 1239) generally have a very thick outer wall, which is often produced in advance of the first ridge; their transverse ridges are but slightly bent, and are intimately connected with the outer wall; the upper premolars are usually nearly or quite as complex as the true molars; the lower cheek-teeth are more or less completely

crescentoid; and in all the forms in which that tooth is known there is no third lobe to the last lower true molar. The height of the cheek-teeth varies considerably, their crowns being tallest in *Elasmotherium*. One or more dermal horns may be attached to the fronto-nasal region; and when two of these appendages are present they may be either placed one behind another in the middle line, or in a pair on either side of this line. The digits of the pes are apparently always three, but there may be either three or four in the manus. One of the most generalised forms is *Hyracodon*, from the Lower Miocene of Nebraska, in which the dental formula is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{4}{4}$, $M.\frac{3}{3}$. There were apparently only three digits; the neck and limbs were slender and Horse-like; and there was no trace of a nasal horn. This genus was in all probability a descendant of the Lophiodont *Hyrachyus*, but does not appear to have been the progenitor of the true Rhinoceroses. In some respects still more generalised is the genus *Amynodon* (*Orthocynodon*), from the Middle and Upper Eocene of North America, in which the dental formula was the same as in *Hyracodon*. The lower canines were nearly upright; there was a short diastema; the premolars were unlike the true molars; and it is believed that the manus had four digits. Allied to this genus is *Metamynodon*, from the Miocene of the United States, in which the skull (fig. 1237) has a strong sagittal crest, the premolars are reduced to $\frac{3}{2}$, the lower canines have become somewhat proclivous, and the upper premolars are much more like the true molars. These two genera are regarded by some of the American palæontologists as indicating a distinct family—the *Amynodontidæ* — and are also looked upon as the ancestors of the true Rhinoceroses. In the Old World there is, however, the genus *Cadurcotherium* of the Quercy Phosphorites, which may possibly lay claim to this position, although it may indicate a lateral branch allied to the Toxodontia. Unfortunately, only detached teeth are at present known, so that the dental formula cannot be determined. The upper true molars (fig. 1238)

Fig. 1238. — A left upper true molar of *Cadurcotherium cayluxense*; from the Upper Eocene of France.

are Rhinocerotic in structure, but are extremely narrow in a transverse direction, and the ridges of the lower cheek-teeth are imperfectly crescentoid. Apparently nearly related to the preceding is *Homalodontotherium*, from Tertiary strata of unknown age in Patagonia; the dental formula is the typical one, and there is no diastema, but the skeleton is unknown. We now come to the consideration of those animals which we may term true Rhinoceroses—a group in which very diverse views as to the limits of generic terms are prevalent among zoologists and palæontologists. By some writers the five existing species are referred to at least three distinct genera; and if this view be adopted, it will be necessary to make a large number of genera for the extinct forms; the English school, however, now generally include all the living species in one genus, and from this point of view there seems no good reasons for generically separating any of the extinct species, which form a series so intimately connected that it would be very difficult to define all the genera into which they are divided by the American school.[1] Using, then, the term *Rhinoceros* in its widest sense, the variations in the number of teeth may be expressed by the formula $I.\frac{(0-2)}{(0-1)}$, $C.\frac{0}{(0-1)}$, $Pm.\frac{4}{4}$, $M.\frac{3}{3}$; the absence of upper canines is a distinctive feature; the upper true molars (fig. 1239) have their crowns relatively wide, their transverse ridges well developed, the hinder lobe of the last

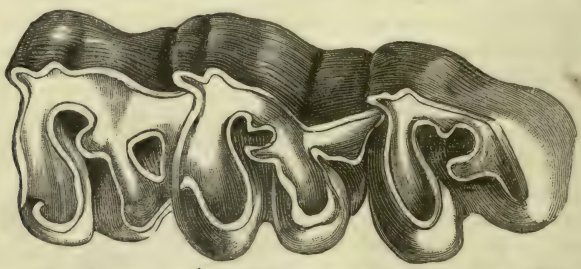


Fig. 1239.—The left upper true molars of *Rhinoceros megarhinus*; from the Pleistocene of England. One-half natural size.

tooth partially aborted, and frequently a more or less distinct buttress at their antero-external angle. The teeth represented in fig. 1239 are the most generalised type; and it is evident that, when more

[1] In this and other instances the number of generic divisions which we may be disposed to adopt is solely a matter of convenience. From the writer's point of view the multiplication of generic terms, which as our knowledge advances must become less and less susceptible of exact definition, tends to drown the science in a sea of names, which form a great burden to the memory, and thus tend to destroy the very object of classification.

worn, the crown of each molar would carry two isolated fossettes surrounded by enamel (fig. 1244). The worn crown-surface is transversely ridged; and there is a process projecting from the hinder ridge into the middle valley termed the crochet, which is absent in some species. The hinder premolars are as complex as the true molars; and the crowns of the cheek-teeth, though varying in height, are never very tall, and their valleys are always open. In the lower cheek-teeth the ridges form complete crescents, with their concavity directed inwardly (fig. 1240). The lower canines are always proclivous. The skeleton and skull are very massive, this feature being most marked in the more specialised species. This genus may be divided into several groups, of which the *Aceratherine* is the most generalised. In this group there is usually no horn, and the nasal bones (fig. 1241) are consequently small; cutting-teeth are always present, although there is some variation in their number, which may be expressed by the formula $I.\ \frac{(0-2)}{1}$, $C.\ \frac{0}{1}$. In *R. incisivus* (which is the type of the so-called *Aceratherium*) there are four digits in the manus; but in many of the North American forms (which on this account are separated by Professor Cope under the name *Aphelops*, fig. 1242) the number of digits was reduced to three; and these forms were thus similar to some female examples of the existing *R. sondaicus*, in which the horn is absent. In Europe this group ranges from the Lower Mio-

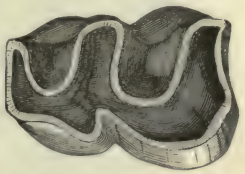


Fig. 1240.—The third left lower true molar of *Rhinoceros megarhinus;* Pleistocene. Two-thirds natural size.

Fig. 1241.—Cranium of *Rhinoceros incisivus:* from the Lower Pliocene of Germany. One-seventh natural size. (After Kaup.)

cene to the Lower Pliocene; it also occurs in the Upper Miocene and Pliocene of India, and in the Upper Miocene (or ? Pliocene) of North America. In the *Diceratherine* group (*Diceratherium* of

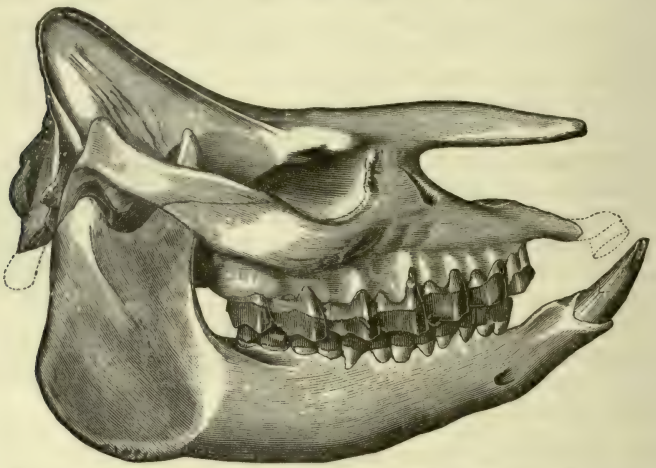


Fig. 1242.—Skull of *Rhinoceros megalodus;* from the Upper Miocene of Colorado. One-sixth natural size. (After Cope.)

Marsh) there was a transversely-placed pair of small nasal horns; the formula of the cheek-teeth being $I.\ \frac{1}{1}$, $C.\ \frac{0}{1}$: it is represented in the Lower Miocene of Europe by *R. minutus*, and by another species in North America. At this stage of evolution the genus disappeared from the latter country.

The *Rhinocerotine* group is characterised by the presence of a single well-developed nasal horn,[1] and of cutting-teeth in both jaws. It is represented at the present day by the Asiatic *R. sondaicus* and *R. unicornis* (fig. 1243), the upper true molars of the former being of the type of those of *R. megarhinus* (fig. 1239), while those of the latter are of the more specialised type of *R. antiquitatis* (fig. 1245). The ancestor of *R. sondaicus* is probably to be found in *R. sivalensis*, of the Pliocene of India; while *R. palæindicus* appears to be the species from which *R. unicornis* has sprung. The *Ceratorhine* group, represented by the existing Asiatic *R. sumatrensis*, and the European Lower Pliocene *R. Schleiermacheri*, differs from the preceding by having two horns, placed one behind the other in the median line, but still retains cutting-teeth in both jaws; the upper

[1] The horn of the Rhinoceroses, it should be observed, consists merely of a bundle of closely agglomerated bristles, and has no bony attachment to the skull.

molars in both species being of the type of fig. 1239. This group cannot probably be separated from the next, with which it is connected by *R. persiæ*, of the Pliocene of Maragha in Persia, which had lower canines, although apparently allied to *R. platyrhinus*. The most specialised, or *Atelodine*, group is represented at the

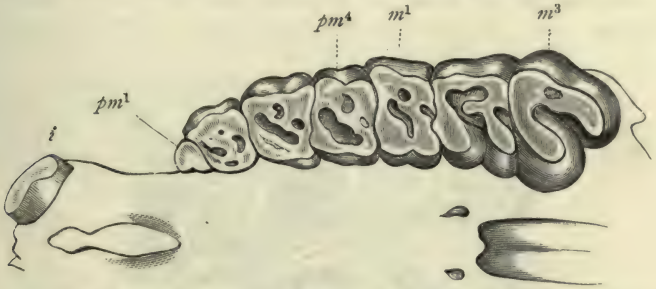


Fig. 1243.—Worn left upper dentition of *Rhinoceros unicornis*; India. Much reduced. (After Cuvier.)

present day by the African *R. simus* and *R. bicornis*, in which there are two large horns, but no cutting-teeth in either jaw. Of species with upper molars of the simpler type of fig. 1239, we may mention *R. pachygnathus*, of the Lower Pliocene of Greece and the isle of Samos, which is closely allied to the African *R. bicornis*; *R. etruscus* (fig. 1244), of the Upper Pliocene of Europe (in which

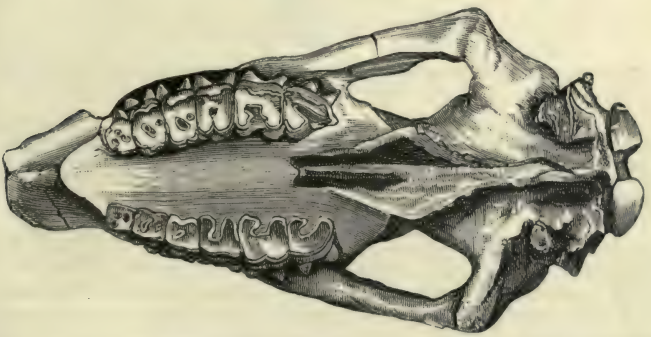


Fig. 1244.—Palatal view of the cranium of *Rhinoceros etruscus*, with the teeth much worn; Upper Pliocene, Italy. One-seventh natural size.

the molars are of a brachydont structure); *R. deccanensis* and *R. karnuliensis*, of the Pleistocene of Southern India; and *R. megarhinus* (fig. 1239) and *R. leptorhinus*, of the European Pleistocene. In the latter there is an ossification of the nasal septum. The other members of this group have their upper molars (fig. 1245) of

a more complex type; there being an absence of a buttress at the antero-external angle, and the folds of the crown so arranged that when more worn than in the figured specimen three islands of enamel would be formed on their crowns. These teeth are also characterised by their plane of wear being perfectly horizontal, and by their relatively tall crowns. An early member of this type is *R. platyrhinus*, of the Pliocene of Northern India; from which species

Fig. 1245.—The second right upper true molar of *Rhinoceros antiquitatis*; from the Pleistocene of Kent.

it is highly probable that both the existing African *R. simus*, and the Pleistocene *R. antiquitatis*, of Northern Asia and Europe, have been derived.

The latter species, of which the skull is represented in fig. 1246 and an upper molar in fig. 1245, is sometimes known as the Woolly Rhinoceros, since it was covered with a thick coat of woolly hair. The skin was devoid of the folds which characterise the large Indian species; and the front horn was of very large size. As in some of the Pleistocene species the septum of the nares was completely ossified (fig. 1246). This species is essentially a northern form, and has nearly the same distribution as the Mammoth, although it does not appear to have crossed Behring Strait into America. In time this Rhinoceros makes its first appearance in the Pleistocene Brick-earths of the Thames valley, and is very common in European cave-deposits, and in the *tundras* of Siberia. Complete carcasses, still covered with the dried flesh, skin, and hair, have not unfrequently been found washed out from the frozen alluvial deposits of these *tundras* on the banks of the Yenesi and Lena; from which we learn that

the food of this animal mainly consisted of the leaves and twigs of juniper and other coniferous plants.

The last representative of this family is the gigantic *Elasmotherium* (*Stereoceros*) of the Pleistocene of Siberia, in which the dental formula of the adult is $I.\ \frac{0}{0}$, $C.\ \frac{0}{0}$, $Pm.\ \frac{2}{2}$, $M.\ \frac{3}{3}$. The structure of the skull and limbs is essentially Rhinocerotic; and in the former the narial septum was completely ossified, and the frontals have a huge bony protuberance for the support of a large horn corresponding to the second one of *Rhinoceros antiquitatis*. The teeth differ considerably from those of any species of *Rhinoceros*,

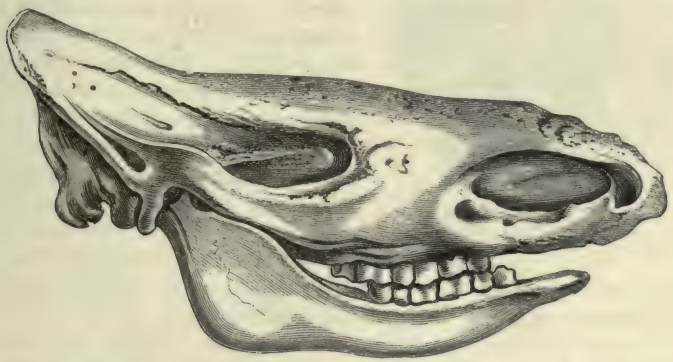


Fig. 1246.—Right lateral aspect of the skull of a young individual of *Rhinoceros antiquitatis*; from the Pleistocene of Siberia. Reduced.

and are characterised by their very tall crowns, plicated enamel, and smooth plane of wear. Their structure is, however, merely an extreme modification of the Rhinocerotic type, to which the nearest approach among later forms is made by *R. antiquitatis*. There is, however, in these teeth a marked resemblance to those of *Cadurcotherium* and *Homalodontotherium*, and it is not improbable that *Elasmotherium* presents the last representative of a stock descended from the former genus which has remained altogether apart from the true Rhinoceroses.

Family Lambdotheriidæ.—With the *Lambdotheriidæ* we enter upon the consideration of the first of three extinct families in which the cheek-teeth have remarkably short (brachydont) crowns, and diverge to a certain extent from the more typical Lophodont form. The upper true molars (fig. 1247) may be described as consisting of four columns, of which the two hindmost are frequently connected by an oblique transverse ridge; while there may also be a more incomplete anterior ridge. When these teeth are worn two

V-shaped surfaces of dentine appear on the crown. This type of tooth may be derived from the Lophodont by the more or less complete abortion of the middle portions of the transverse ridges. The upper premolars are simpler than the true molars, and have but a single inner column; while the lower cheek-teeth are crescentoid, the last true molar usually not having a complete third lobe. There was always a diastema in the dental series, and the skull was devoid of bony protuberances. In the present North American family the femur has a third trochanter, and the feet are of the normal Perissodactylate type, the manus being provided with four, and the pes with three digits. This family is represented by *Palæosyops* and *Limnotherium*, from the Upper Eocene, in which there are four premolars, and the last lower true molar has a third lobe; the canines being large and resembling those of the Carnivora. *Lambdotherium* is another form of later age; while in the White-river Miocene of Canada we have *Haplacodon*, with only two pairs of lower incisors.

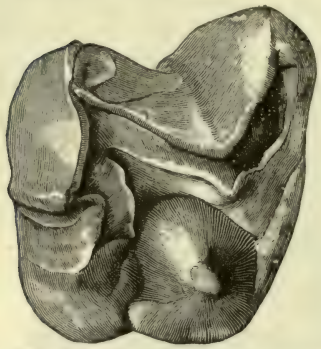


Fig. 1247.—The third right upper true molar of *Chalicotherium sinense;* from the Pliocene of China.

Family Chalicotheriidæ. — The second family, or *Chalicotheriidæ*, is found in both the Old and the New Worlds, and presents such a remarkable abnormality in the structure of the feet, as to render it for the future quite unsafe to predict the character of an animal from a single bone, and to make invalid the old maxim *ex ungue leonem*. In the femur the third trochanter has been lost; and in the feet, while the proximal bones retain their normal Perissodactylate character, the phalangeals have been modified to resemble those of Edentates, the second phalangeal (fig. 1248) having a strongly developed distal trochlea for the articulation of the huge claw forming the terminal joint. These phalangeals have been described under the names of *Macrotherium* and *Ancylotherium*, and were until quite recently, when they were found by Dr Filhol in association with the skull and the rest

Fig. 1248.—Anterior and distal aspects of a second phalangeal of *Chalicotherium sivalense;* from the Siwaliks.

of the skeleton of *Chalicotherium*, thought to belong to huge Edentates. The latter writer has indeed proposed to regard this genus as a veritable Edentate, but the resemblance of its dentition to that of *Palæosyops*, coupled with the essentially Perissodactylate characters of the rest of the skeleton — notably the opisthocœlous cervical vertebræ — prevents the acceptation of this view, and compels us to regard this strange animal as a highly modified and aberrant Ungulate.[1] In the type genus *Chalicotherium*, with which *Macrotherium* is identical, there were variations in the number of the cutting-teeth analogous to those obtaining in *Rhinoceros*, which may be expressed by the formula $I.\ \frac{(0-3)}{(0-3)}$, $C.\ \frac{(0-1)}{1}$, $Pm.\ \frac{3}{3}$, $M.\ \frac{3}{3}$. The type species, which should be known as *C. giganteum*, occurs typically in the Lower Pliocene of Eppelsheim in Hessen-Darmstadt, and also in the Middle Miocene of Sansan in Gers; the claws were first described by Cuvier under the name of *Pangolin gigantesque*, and were subsequently made the type of the genus *Macrotherium*. Another species, *C. modicum*, occurs in the Upper Eocene Phosphorites of France, to which probably belong some large claws described as those of an Edentate. The genus also occurs in the Pliocene of China and India; the species from the latter area having been referred by Kaup to a distinct genus *Nestoritherium*, on account of the absence of the anterior teeth. The phalangeal from the Pliocene of Sind represented in fig. 1248 doubtless belongs to a small individual of this species, although first described as *Manis*, and subsequently as *Macrotherium*. It has likewise been lately recorded from the White-river Miocene of Canada and the Loup-Fork beds of Kansas. The last lower molar of *Chalicotherium* has no third lobe. From the Lower Pliocene of Attica the genus *Leptodon*, described on the evidence of a lower jaw with a Chalicotheroid dentition, but with a third lobe to the last molar, is probably identical with *Ancylotherium*, founded upon the evidence of claws from the same beds, which are of the same general type as those of the so-called *Macrotherium*. *Ancylotherium* also occurs in the Lower Pliocene of the isle of Samos. *Leptodon* has been provisionally referred by Dr Schlosser to the next family. *Moropus*, from the Loup-Fork of Kansas, and *Morotherium*, from the Miocene of the United States, which were described by Professor Marsh as Edentates, are probably closely allied to, if not identical with, either *Chalicotherium* or *Ancylotherium*. Finally, the imperfectly known *Brachydiastematotherium*, from the Eocene of Hungary, is probably

[1] Professor Cope has recently proposed to make *Chalicotherium* the type of a distinct order under the name of Ancylopoda.

referable to the present family, which is evidently a very ancient branch of the suborder, and may, it is suggested, have been directly derived from the Condylarthra.

Family Titanotheriidæ.—This extinct family, equivalent to the *Brontotheriidæ* of Professor Marsh and the *Menodontidæ*[1] of several other writers, is so closely connected by *Diplacodon* with the *Lambdotheriidæ*, that Dr Schlosser has proposed to unite the two. In the present family at least the fourth upper premolar has two inner columns, and is thus as complex as the true molars; while in those forms of which the limbs are known there are four anterior and three posterior digits. The third trochanter of the femur is rudimentary. Paired bony protuberances may be present in the fronto-nasal region of the skull. In *Diplacodon*, of the Eocene of North America, only the fourth upper premolar is as complex as the true molar; the canines are as large as in *Palæosyops;* the incisors $\frac{(3)}{(3)}$ are small; and the skull has no bony protuberances.

The type genus *Titanotherium*, which Messrs Scott and Osborn consider should include *Menodus* (preoccupied), *Megacerops*, *Brontotherium*, *Diconodon*, and probably *Symborodon*, is confined to the

Fig. 1249.—Left lateral aspect of the cranium of *Titanotherium coloradense;* from the Miocene of North America. Greatly reduced. (After Marsh.)

Miocene of North America, and comprises animals of huge bulk; and it is probable that the forms recently described by Professor Marsh under the names of *Allops*, *Brontops* (fig. 1250), and *Menops* are not really separable. An entire skeleton is shown in fig. 1250, and a cranium in fig. 1249. The number of teeth is subject to a variation analogous to that obtaining in *Rhinoceros*, this variation being expressed by the formula $I.\ \frac{(2-3)}{(0-3)}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{4}{(3-4)}$, $M.\ \frac{3}{3}$.

[1] The name *Menodus* is the earliest of those applied to these animals, but is inadmissible on account of the earlier application of *Menodon* to a fossil reptile.

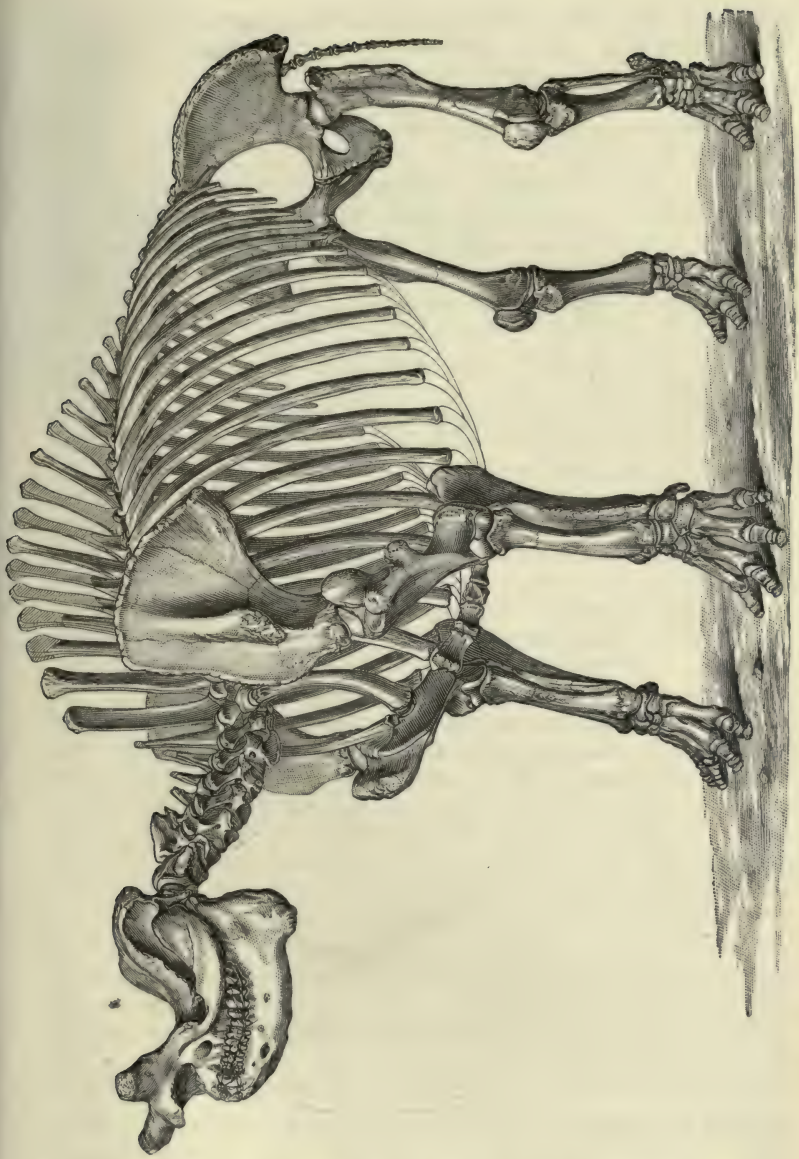


Fig. 1250.—Skeleton of *Titanotherium* (*Brontops*) *robustum*; from the Miocene of North America. $\frac{1}{24}$ natural size. (After Marsh.)

The molars and premolars are alike, the incisors are small, and in those species with a full dentition there is no diastema; while in the typical forms the canines are small. The cranium (fig. 1249) is

elongated, with a small brain-cavity, projecting nasals, and a pair of stout transversely placed prominences on the fronto-nasal region. A form to which the name *Dæodon* has been applied is distinguished by the larger canines. It has been suggested that the American *Meniscotherium* and the European *Hyracodontotherium* should be placed in this family.

Family Macraucheniidæ.—Here may be placed this remarkable family, which presents extremely generalised characters in the vertebræ and limb-bones, such as are unknown in any other members of the suborder, on which account some writers think it ought not to be included in the Perissodactyla. In the typical *Macrauchenia* from the Pleistocene of South America the dentition is $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{4}{4}$, $M.\frac{3}{3}$; the cheek-teeth are Rhinocerotine in structure, the upper molars showing two external V-shaped dentine surfaces and two transverse ridges; while there is only a very small diastema in the lower jaw. The cervical vertebræ resemble those of the *Camelidæ* in the position of their arterial canal. The fibula articulates with the calcaneum (as in the Artiodactyla), and there are three digits in each foot, of which the lateral ones are of large size. The incisors have a deep coronal infolding of the enamel, as in the *Equidæ;* and Dr Hermann Burmeister thinks that the muzzle was produced into a short proboscis. The type species is *M. patachonicha;* an allied form from the infra-Pampean beds of Argentina, named by Bravard *Palæotherium paranense*, is referred by Dr Burmeister to this genus, but has been made the type of a distinct genus by Dr Ameghino, under the name of *Scalibrinitherium Bravardi*. *M. minuta* from the same deposits is made by the latter writer the type of *Oxydontotherium;* and the name *Mesorhinus* is applied to yet another form from the same area. Here also may be noticed *Theosodon* from the above-mentioned deposits, which is placed by Dr Ameghino in this family, although it may be allied to *Homalodontotherium*, which is also placed here by that writer.

Suborder 3. Toxodontia.—This group includes a number of very aberrant and generalised Ungulates from the Tertiaries of South America, which present affinities to the Perissodactyla, Proboscidea, and Rodentia, and consequently render it almost impossible to draw up any distinctive diagnosis.

Family Toxodontidæ.—*Nesodon* from strata of unknown Tertiary age in *Patagonia* has its dental formula $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{4}{4}$, $M.\frac{3}{3}$; the incisors having short crowns, and the true molars a complex Rhinoceroid structure, and thus connecting the dentition of *Macrauchenia* and *Homalodontotherium* with that of the next genus. The small *N. ovinus* was about the size of a Sheep; but its limb-bones

are unknown. In *Toxodon*, of which the type species is of large size and is found in the Pleistocene of Argentina, the dental formula is $I.\frac{2}{3}$, $C.\frac{0}{1}$, $Pm.\frac{4}{3}$, $M.\frac{3}{3}$. All the teeth (fig. 1251) grow from persistent pulps; the lower canines are very minute, the incisors large, and the crowns of both the latter and of the cheek-teeth strongly curved. The structure of the latter is a simplification of the plan obtaining in *Nesodon*. The femur has no third trochanter, the fibula articulates with the calcaneum, and the cranium approximates in some respects to that of the *Suidæ*. In the typical *T. platensis* the outermost upper incisor is the larger of the two, the

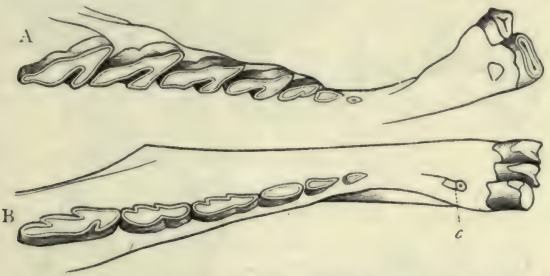


Fig. 1251.—Oral surfaces of the right upper (A) and lower (B) dentition of *Toxodon Burmeisteri*; from the Pleistocene of the Argentine Republic. Much reduced. *c*, The lower canine.

reverse condition obtaining in *T. Burmeisteri* (fig. 1251). From the infra-Pampean deposits Dr Ameghino has recently described various remains of allied forms under the names of *Toxodontotherium*, *Haplodontotherium*, and *Dilobodon*. A mandible from the Tertiary of Monte Hermosa, in Argentina, is characterised by the triangular form of the third incisor, and has accordingly been named *Trigodon* by Dr Ameghino. Dr Moreno states, however, that this mandible belongs to the same animal as the teeth described as *Toxodontotherium* and *Haplodontotherium*; and he would adopt for their owner the name *Trigodon* as the one which was alone well defined.[1] The type mandible is peculiar in having only a single median incisor, placed on the line of symphysis, but this is probably an individual abnormality. Apparently more nearly allied to *Nesodon* (which Dr Ameghino makes the type of a distinct family) are *Colpodon* and *Protoxodon*; while other allied remains described by the same writer from the Tertiaries of Argentina under the names of *Interatherium*, *Toxodontophanes*, and *Tembotherium*, are referred to two distinct families.

Family Typotheriidæ.—Perhaps still more remarkable is *Typo-*

[1] This name is really preoccupied by the earlier *Trigonodon* and *Trigonodus*.

therium (*Mesotherium*) from the infra-Pampean beds of Argentina, in which the dentition is *I.* $\frac{1}{2}$, *C.* $\frac{0}{0}$, *Pm.* $\frac{2}{1}$, *M.* $\frac{3}{3}$. The incisors grow from persistent pulps; and the structure of the cheek-teeth recalls that of *Toxodon*. The skull (fig. 1252) is of an Ungulate type; there is a third trochanter to the femur; and clavicles

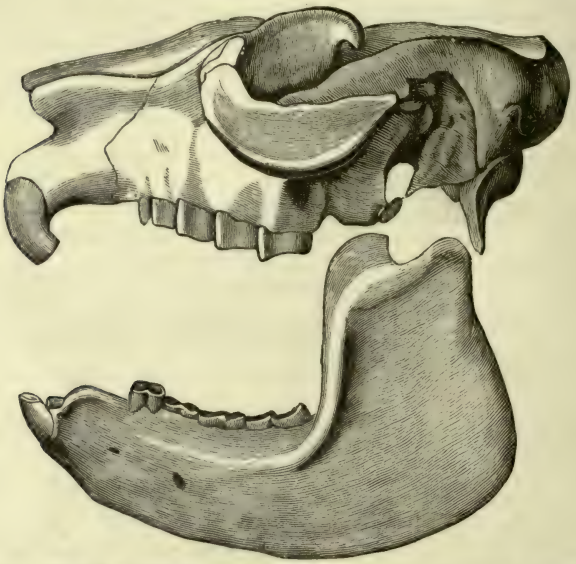


Fig. 1252.—Skull of *Typotherium cristatum*; from the infra-Pampean of Argentina. One-half natural size.

(which are unknown in any other Ungulate) are present. This peculiar genus presents characters connecting the *Toxodontidæ* with the Rodents. Allied forms from the infra-Pampean deposits of the same region have been described as *Protypotherium*, *Stenotephanus*, and *Tomodus*; while *Pachyrucus* from the later Tertiary of Monte Hermosa is a much smaller form with three premolars.

Suborder 4. Condylarthra.—This group comprises a number of very generalised Ungulates mostly from the Eocene of North America, which are grouped by Professor Cope, on account of the structure of their feet, with the Hyracoidea in a division termed Taxeopoda.[1] Both the present group and the Hyracoidea are characterised by the scaphoid of the carpus being supported by the trapezoid and not by the magnum, which carries the lunar; while in the tarsus the cuboid articulates proximally with the calcaneum

[1] Professor Cope would also include the Primates among the Taxeopoda.

only. There is but slight mutual interlocking of the carpal and tarsal bones; the structure of these joints being simpler than in the other suborders, and resembling those of the Unguiculate orders. In the Condylarthra the dental formula is nearly always the typical one; the cheek-teeth are brachydont, and usually bunodont, although rarely lophodont. The premolars are simpler than the true molars, which may be tritubercular like those of many Carnivora; the canines and incisors frequently also recall those of that order. The humerus is peculiar among Ungulates in having an entepicondylar foramen; the femur has a third trochanter; the astragalus, as in the Carnivora, presents a uniformly convex distal articular surface; and there is no articular facet for the fibula either on this bone or on the calcaneum. The feet usually have five digits, with sharply pointed terminal phalangeals; and the radius and ulna are distinct. This suborder may be regarded as containing the ancestral types from which the Artiodactyla and Perissodactyla have sprung. It further presents such remarkable signs of affinity (especially in the structure of the teeth, the form of the astragalus, and the presence of the foramen in the humerus) with the Carnivora, that it seems highly probable that we may look upon the Condylarthra as a side branch from the original ancestral stock of the Carnivora, which is most nearly represented by the more primitive Creodonts.

Family Periptychidæ.—In this the most generalised family the dentition is bunodont; the digits are five on each foot; the astra-

Fig. 1253.—*Periptychus rhabdodon.* Right upper (*a*) and lower (*b*) cheek-dentition, grinding surface; from the Puerco Eocene of New Mexico. Two-thirds natural size. (After Cope.)

galus has no trochlea; and the premolars are very simple. In the type genus *Periptychus*, from the Lowest, or Puerco, Eocene of New Mexico, the dental formula is $I.\ \frac{(2-3)}{3}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{4}{4}$, $M.\ \frac{3}{3}$, and the incisors and lower canines are small. The typical *P. rhabdodon*

(fig. 1253) is characterised by its vertically grooved premolars. Other genera from the North American Eocene are *Hexodon*, *Ectoconus*, *Anisonchus*, *Hemithlæus*, *Haploconus*, and *Zetodon;* of which the fourth may be not separable from the third. From this family Dr Schlosser regards the bunodont Artiodactyla as derived, and thinks a direct relationship can be traced from *Periptychus* to *Achænodon*, and thus to the other *Chæropotamidæ*. The humerus is short, and much expanded distally.

Family Phenacodontidæ.—In this family the brain (fig. 1254) is characterised by the extremely small size of the hemispheres,

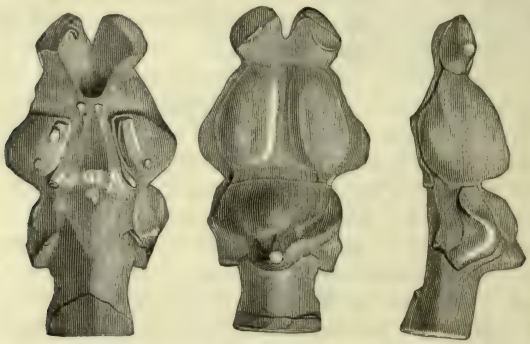


Fig. 1254.—Inferior, superior, and left lateral aspects of the brain of *Phenacodus primævus;* from the Lower Eocene of North America. (After Cope.)

which are only one-fourth longer than the cerebellum, and thus indicate a very low type of organisation. The family is readily distinguished from the preceding by having a proximal trochlea to the astragalus, by the longer neck, and less simple premolars, which are, however, different from those of the following family. The type genus *Phenacodus* (fig. 1255) includes several species from the Puerco and Wasatch Eocene of North America, varying from the size of a small terrier to that of a leopard. The dental series comprises the full typical number; and although the crowns of the upper true molars are of a bunodont structure, yet they could be readily modified into the lophodont type of *Hyracotherium*, and we must probably regard the latter as a direct descendant of the present genus, with perhaps the intervention of *Systemodon*. Professor Rütimeyer has described some upper molars from the Upper Eocene of Switzerland which he refers to *Phenacodus*, although they are much more of a lophodont type than in the American species.

Professor Cope remarks of one of the species of *Phenacodus* that "the size of the animal is about that of a Bull-dog, but the head is smaller,

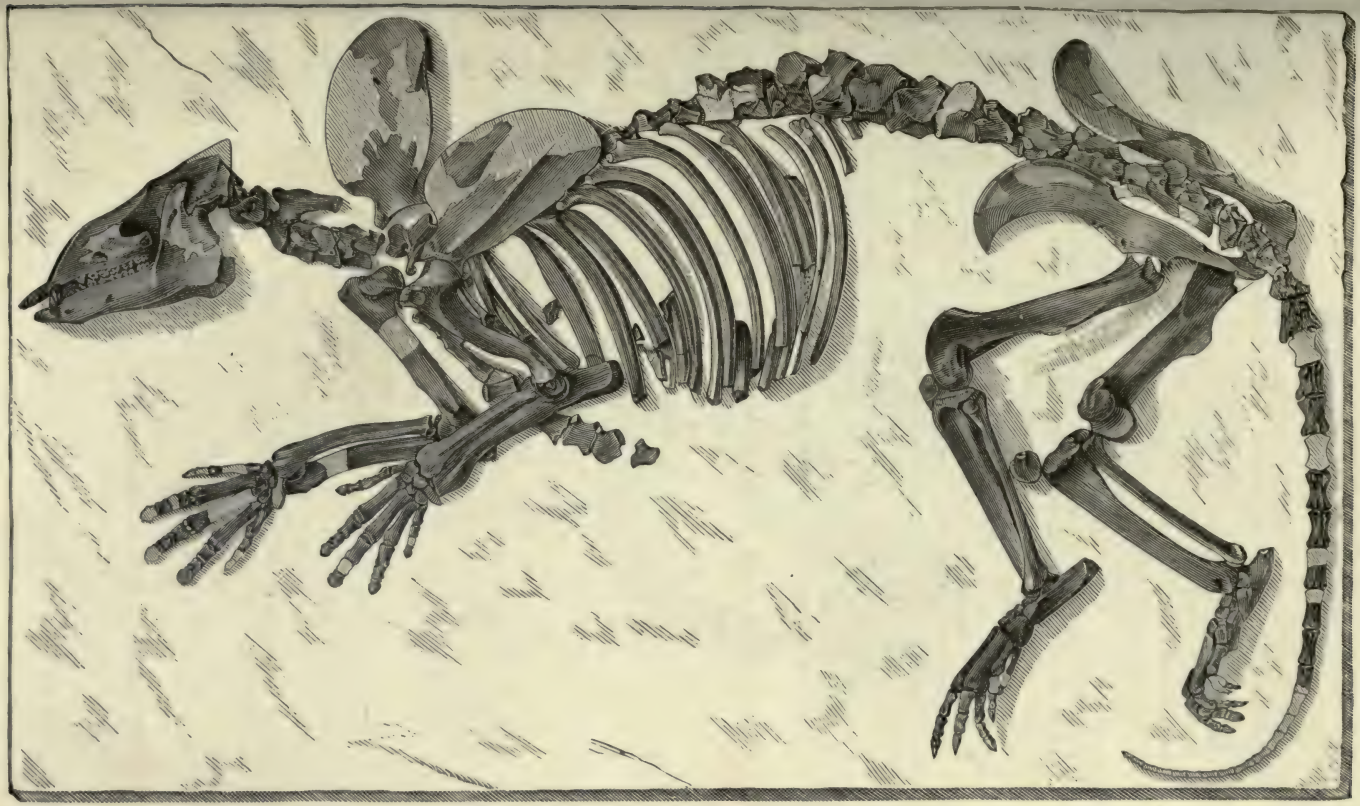


Fig. 1255.—Slab of rock showing the left lateral aspect of the skeleton of *Phenacodus primævus;* from the Lower Eocene of North America. One-seventh natural size. (After Cope.)

and the neck rather shorter and not nearly so robust. The limbs have about the same proportions to the body as those of a Bull-dog, but the anterior ones are shorter. The proportions of the parts of the limbs, and of the fore and hind limbs to each other, excepting the feet, are much as in the Collared Peccary. . . . We can thus imagine the *Phenacodus Vortmani* as an animal of the comparatively slender build of the Bull-dog, with a head and neck proportioned more as in the Racoon, and with the rump more elevated than the withers, as in the Peccary. The feet resembled those of a Tapir or Rhinoceros, but had an [additional] pair of short toes on each foot, which did not reach the ground. To this add a tail much like a Cat's in proportions, and the picture is complete. In diet the animal was omnivorous, the proportions of animal food being smaller than the Hogs, for instance, use. The food is more likely to have resembled that of the Primates. What means of defence this species had is not easily surmised, as the canine teeth and hoofs are not large."

The species represented in the accompanying woodcut was of larger dimensions; Professor Cope stating that it was intermediate in size between a Sheep and a Tapir. Comparing it to an animal with an equally long tail, we might perhaps take a Leopard as a fair representative. The remarkable length of the tail at once shows a wide difference from all existing Ungulates. Professor Cope, from the structure of the bones of the nasal region, suggests that the head may have had a short proboscis.

Other genera from the American Eocene are *Protogonia*, *Anacodon*, and *Diacodexis*. The former occurs in the Puerco, and typically has but one outer tubercle to the fourth premolar, in place of the two of *Phenacodus*. Professor Rütimeyer refers to this genus teeth from the Upper Eocene of Switzerland.

Family Meniscotheriidæ.—This family is taken to include two genera characterised by their lophodont dentition, which are evidently more specialised than the preceding types. By Dr Schlosser they are regarded as allied to the *Chalicotheriidæ*, and there are perhaps indications of affinity between the European genus and the Hyracoidea. The humerus is longer and less expanded than in the *Periptychidæ*, but the number of the digits is unknown. There is no marked diastema in the dental series. The typical genus *Meniscotherium* is from the Wasatch Eocene of New Mexico, and is characterised by its small incisors, and the presence of two outer lobes to the last upper premolar. Teeth from the Swiss Eocene have been referred to this genus. In *Hyracodontotherium*, from the Upper Eocene of France, the upper incisors are large and curved, the first being especially enlarged, and closely resembling the corresponding tooth of *Hyrax;* the canine is small, and resembles the third incisor; while the fourth premolar has but a single outer lobe or tubercle. Two species are known by the skull.

Suborder 5. Hyracoidea.—As mentioned under the head of the Condylarthra, the structure of the carpus and tarsus in the Hyracoidea is the same as in that suborder, but the terminal phalangeals are truncated, and there is an interlocking articulation be-

tween the fibula and astragalus. This suborder is represented solely by the family *Hyracidæ*, containing the two existing genera *Hyrax* (fig. 1256) and *Dendrohyrax;* both of which are confined to Africa and Syria, and are unknown in a fossil condition. The dental formula of the adult is $I.\ \frac{1}{1}$, $C.\ \frac{0}{0}$, $Pm.\ \frac{4}{4}$, $M.\ \frac{3}{3}$; there are four milk-molars; the incisors grow from persistent pulps, and the pattern of the cheek-teeth is of a Rhinocerotic type. The fore-feet have

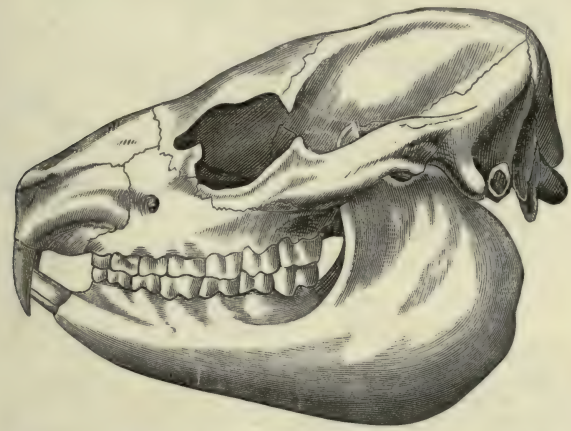


Fig. 1256.—Left lateral aspect of the skull of *Hyrax capensis*. Reduced.

three, and the hind ones four digits; and the terminal phalangeals (except in the inner digit of the pes) have rounded hoof-like nails. The coracoid process of the scapula is well developed; there is no entepicondylar foramen to the humerus; the femur possesses a small third trochanter; and the tibia and fibula are distinct.

Suborder 6. Amblypoda.—In this suborder, which comprises primitive Ungulates of great bulk from the Eocene of Europe and North America, the carpus (fig. 1257, B) is characterised by the scaphoid being supported by the trapezoid and not by the magnum, while the latter and the unciform support the lunar; in the tarsus the cuboid articulates with both the calcaneum and astragalus. The carpus is therefore of a more primitive type than the tarsus. Both the carpal and the tarsal bones interlock to a slight extent (fig. 1257, B, C); the astragalus is flat (fig. 1257, C); the feet are short, plantigrade, and furnished with five digits; and the fibula articulates with the calcaneum. The brain (fig. 1257, A) is very small in proportion to the cranium. The cheek-dentition (fig. 1258) is of a primitive lophodont type; the crowns of all these teeth being very short,

and the upper true molars and the hinder premolars bearing two main oblique ridges, which usually form one or two V's. Upper and lower canines are always present. The pelvis (as seen in fig. 1260) resembles that of the Elephants in the enormous expansion and vertical position of the ilia, but is distinguished by the circumstances that the ischia do not enter into the ventral symphysis. This suborder is usually divided into three sections; but a form

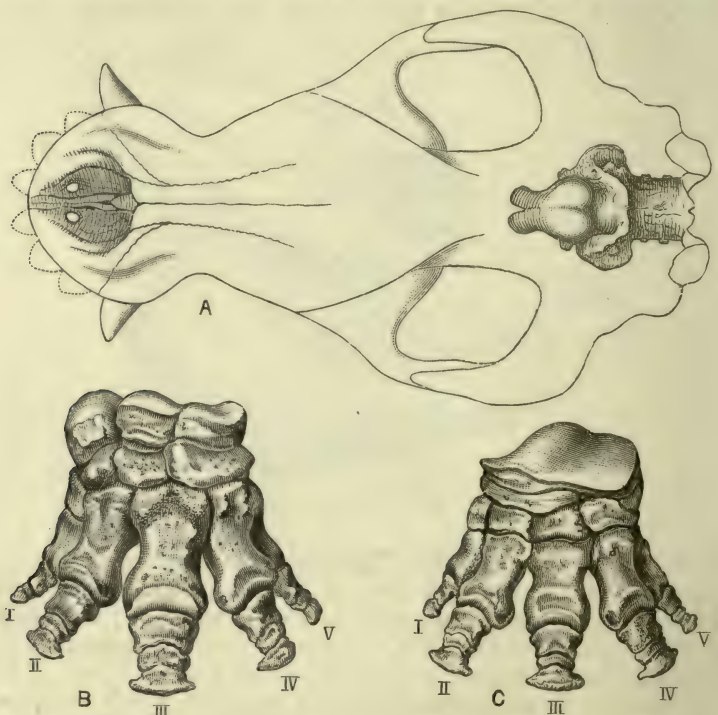


Fig. 1257.—Outline of upper aspect of cranium (A), the left manus (B[1]) and pes (C) of *Coryphodon hamatus*; from the Wasatch Eocene of North America. A, one-fifth, B and C, one-third natural size.

recently discovered in the Bridger Eocene of North America, and named *Elachoceros*, presents characters connecting the last two, and will perhaps render it eventually necessary that they should be abolished. Excluding this form, the characters of the three sections are as follows :—

[1] In the first row of carpal bones the one on the right of the figure is the cuneiform, the central one the lunar, and that on the left the scaphoid ; in the second or lowest row the bone on the right is the unciform, the central one the magnum, and the one on the left the trapezoid.

SECTION A. TALIGRADA.—The astragalus has a head; there is a third trochanter to the femur; and superior incisors are present.

FAMILY PANTOLAMBDIDÆ.—The one family of this section is represented by the genus *Pantolambda*, from the Puerco, or Lowest, Eocene of New Mexico, which presents the feature, quite unique

Fig. 1258.—Left upper cheek-dentition of *Coryphodon hamatus;* from the Wasatch Eocene of North America. One-half natural size. (After Marsh.)

among lophodont Ungulates, of having the upper true molars with narrow subtriangular crowns like those of the premolars of *Coryphodon* (fig. 1258). This is a very important feature, as showing the relationship of the dentition of the Ungulata to that of the Carnivora; and also as indicating that those Ungulates which have the upper premolars as complex as the true molars, are more specialised than those in which the reverse condition obtains.

SECTION B. CORYPHODONTIA.—In this group, which Professor Cope terms Pantodonta, the astragalus has no head; there is a

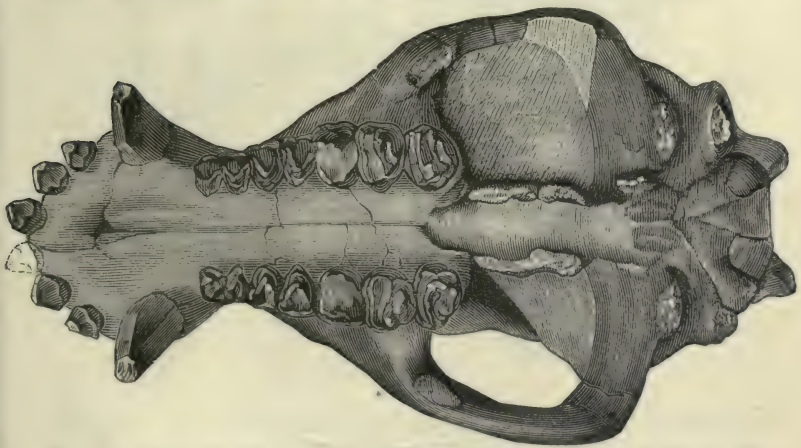


Fig. 1259.—Palatal aspect of the cranium of *Coryphodon hamatus;* from the Wasatch Eocene of New Mexico. Two-ninths natural size. (After Cope.)

third trochanter to the femur; and upper incisors are present. The cranium has no protuberances, and the development of the upper canines is not excessive.

Family Coryphodontidæ.—The upper premolars (fig. 1258) are simpler than the true molars, and there are frequently two V-shaped ridges on the latter. The type genus *Coryphodon* was originally founded by Sir R. Owen upon a lower molar from the London Clay; other teeth were subsequently found in the Lower Eocene of

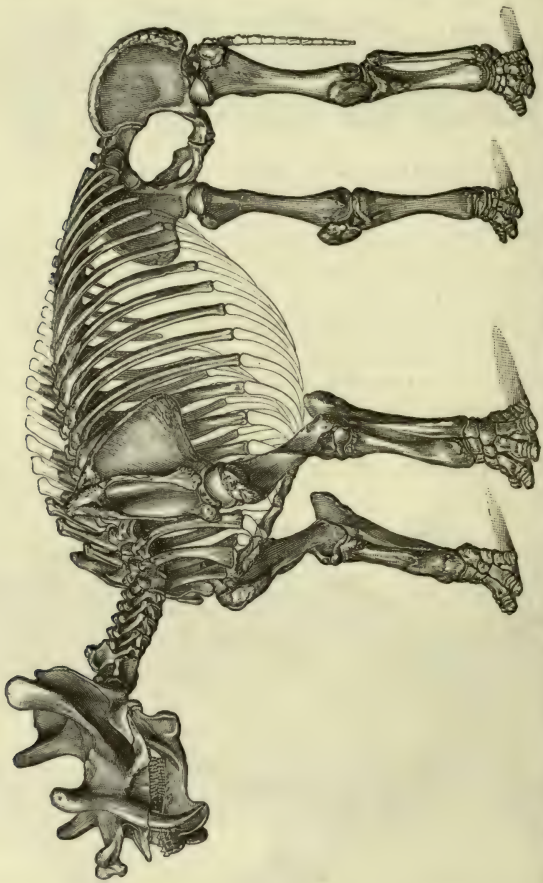


Fig. 1260.—Restoration of the skeleton of *Uintatherium ingens*; from the Bridger Eocene of Wyoming, United States. One-thirtieth natural size. (After Marsh.)

the Continent, but it was reserved for the discoveries in the homologous strata of North America to indicate the full structure of this curious genus. The dentition is *I.* $\frac{3}{3}$, *C.* $\frac{1}{1}$, *Pm.* $\frac{4}{4}$, *M.* $\frac{3}{3}$; and the structure of the upper molars, cranium, and feet is exhibited in the three accompanying woodcuts (figs. 1257-1259.) Other forms from the Eocene of America have received the names of *Metalophodon*

Bathmodon, *Ectacodon*, and *Manteodon;* but further observations are required to show whether all of these are really distinct from the type genus.

Section C. Dinocerata.—The third section of this suborder, which Professor Marsh regards as entitled to rank as a distinct suborder, is represented by the now well-known Dinocerata, which are exclusively confined to the Upper or Bridger Eocene of North America. These animals were ponderous brutes, nearly as bulky as an Elephant, to which group they present many curious points of resemblance. The skull (figs. 1261-1263) bears several large protuberances; and the upper canines of the males were enormously developed (recalling those of the Feline genus *Machærodus*), and were frequently protected from injury by a descending flange developed from the symphysis of the mandible, as is well shown in the figure of the skeleton. A peculiar and characteristic feature is the total absence of upper incisors; while another distinctive character is the want of a third trochanter to the femur, which thus resembles the corresponding bone of the Proboscidea.

Family Uintatheriidæ.—The whole of the members of the

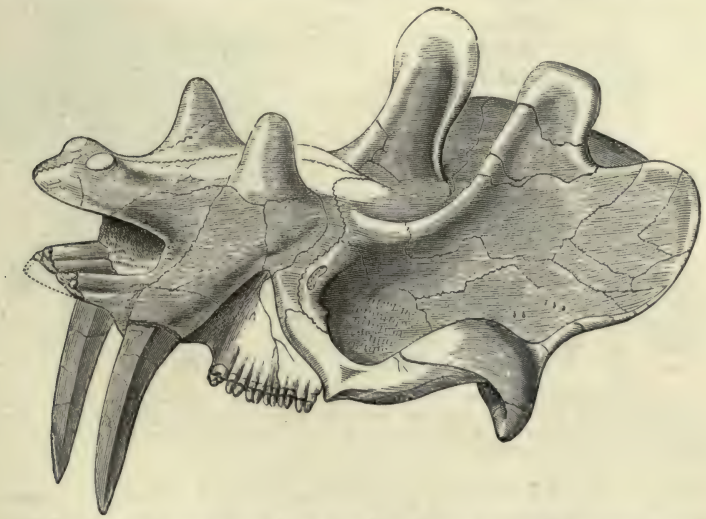


Fig. 1261.—Left lateral view of the skull of *Uintatherium mirabile;* from the Bridger Eocene of Wyoming. Much reduced. (After Marsh.)

section may be included in this family—the equivalent of the *Tinoceratidæ* of Professor Marsh. The hinder upper premolars are as complex as the true molars, and there is no distinct third lobe to the last lower true molar; while in the hinder cheek-teeth of the

upper jaw the two transverse ridges unite on the inner border of the crown to form a V; another V, with its angle directed inwardly, occurring in the corresponding lower teeth. The least specialised genus is *Bathyopsis*, of the lower part of the Bridger Eocene, in which the lower canine is separated from the incisors, and bites in front of the upper canine in the normal manner; thus connecting the more specialised forms with *Coryphodon*. Another form of comparatively small size, distinguished by the absence of nasal prominences, is apparently also entitled to generic distinction, and has been named *Elachoceros*. The typical forms, according to

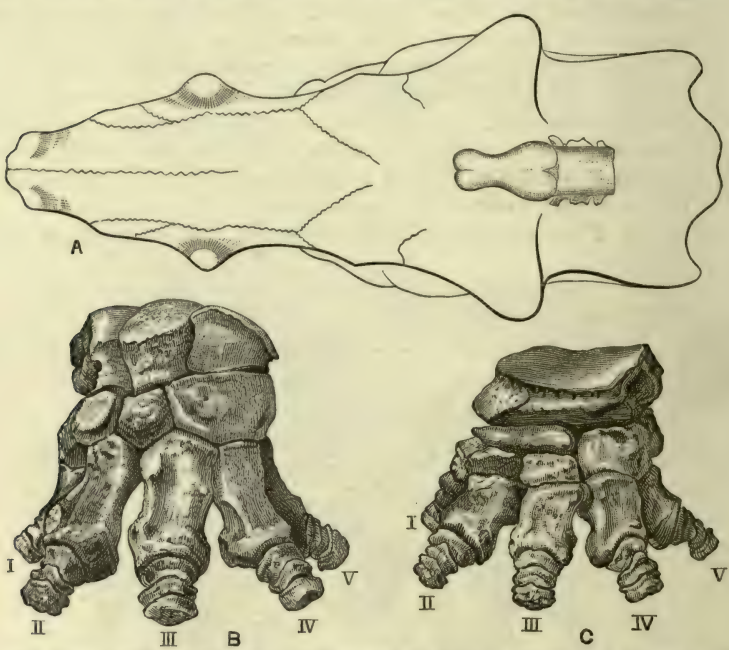


Fig. 1262.—*Uintatherium mirabile;* from the Bridger Eocene. Reduced. A, Frontal aspect of cranium; B, Left manus; C, Left pes. In B the middle bone of the top row is the lunar, while the oval bone on the left of the second row is the trapezoid. The topmost bone in C is the astragalus. (After Marsh.)

Messrs Scott and Osborn, may all be grouped under the generic name of *Uintatherium*, although they have been split up by many writers into several genera under the names of *Dinoceras*, *Octotomus*, *Tinoceras*, *Eobasileus*, and *Loxolophodon*. This genus may be characterised by the presence of nasal tuberosities (fig. 1261), and by the lower canine being approximated to the incisors, which it resembles in structure. The dental formula is usually $I.\ \frac{0}{3}$, $C.\ \frac{1}{1}$,

Pm. $\frac{3}{3}$, *M.* $\frac{3}{3}$; but according to Professor Cope the lower incisors may be wanting. The genus may be divided into a *Dinoceratine* and a *Tinoceratine* group. The former, which includes *Dinoceras* of Marsh and *Octotomus* of Cope, comprises the smaller forms from the typical Bridger, in which the nasals are not greatly produced, and their prominences are comparatively small (figs. 1261, 1262). According to Professor Marsh, the base of the upper canine is vertical, and the lunar has a small facet for articulation with the trapezoid (fig. 1262, B); the neck being comparatively short. In the second group, comprising *Tinoceras* of Marsh, and *Eobasileus* and *Loxolophodon* of Cope, all the species are of huge size, and have the nasals overhanging the premaxillæ, with the prominences very large (figs. 1260, 1262). These species are confined to the upper Bridger, and have the base of the upper canine horizontal, the trapezoid not

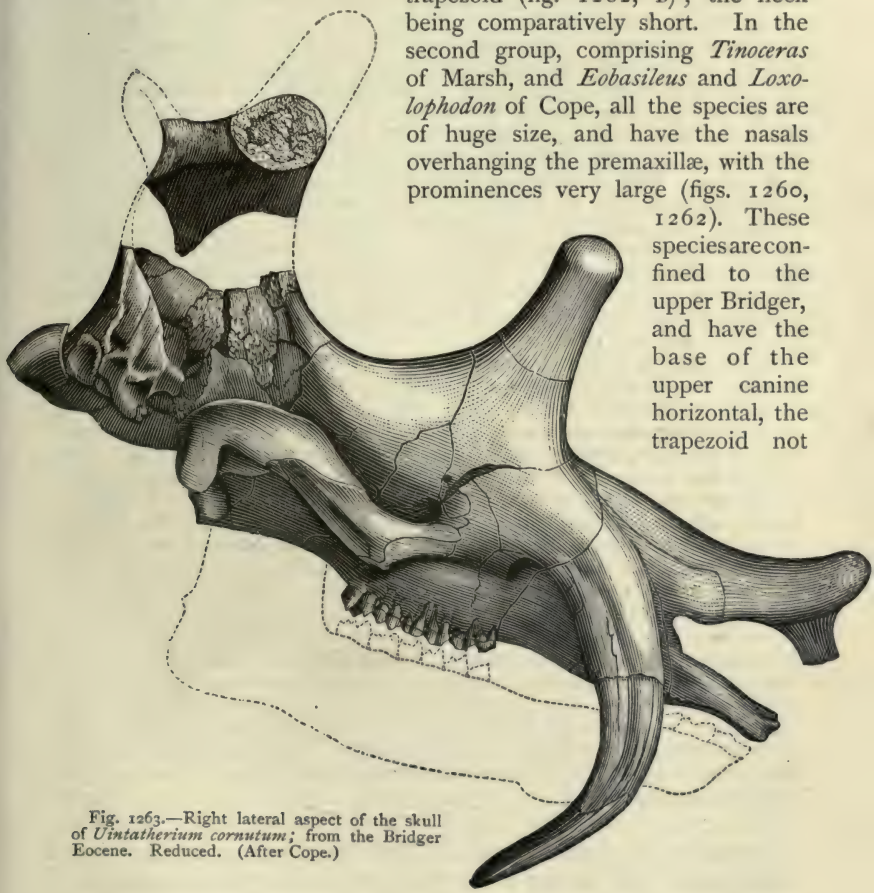


Fig. 1263.—Right lateral aspect of the skull of *Uintatherium cornutum*; from the Bridger Eocene. Reduced. (After Cope.)

articulating with the lunar, and the neck longer. The species, of which the skull is shown in fig. 1262, is remarkable for having the

second pair of prominences placed over the orbit, instead of much further back, as in fig. 1260.

Writing of the Dinocerata Professor Marsh observes that "the fossil remains of this group have hitherto been found in a single Eocene lake-basin of Wyoming, and none are known from any other part of this country or from the Old World. These gigantic beasts, which nearly equalled the Elephant in size, roamed in great numbers about the borders of the ancient tropical lake, in which many of them were entombed. This lake-basin, now drained by the Green River, the main tributary of the Colorado, slowly filled up with sediment, but remained a lake so long that the deposits formed in it, during Eocene time, reached a vertical thickness of more than a mile. . . . At the present time this ancient lake-basin, now 6000 to 8000 feet above the sea, shows evidence of a vast erosion, and probably more than one-half of the deposits once left in it have been washed away, mainly by the action of the Colorado river. What remains forms one of the most picturesque regions in the whole West, veritable *mauvaises terres*, or bad lands, where slow denudation has carved out cliffs, peaks, and columns of the most fantastic shapes and colours. This same action has brought to light the remains of many extinct animals, and the bones of the Dinocerata, from their great size, naturally first attract the attention of the explorer." The latter part of this description recalls to mind the very similar conditions of the Pliocene Siwalik deposits of Northern India, where the place of the bones of Dinocerata is taken by that of Proboscidea. The Professor proceeds to mention that the first remains of these wonderful animals were obtained by him in the year 1870.

In respect to their structure the same writer observes that in the cranium "each maxillary bone carried a well-developed process, probably of the nature of a horn-core. The nasals support two similar but smaller horn-cores; and the frontals are developed behind into two larger bony projections, most probably also of the nature of horn-cores. The animal thus possessed three pairs of horn-cores, one carried by the upper jaw-bones, one by the nasals, and one by the frontal bones. Whether, however, these so-called 'horn-cores' really supported horns, of the nature of the horns of the Cavicorn Ruminants, is quite a matter of conjecture; and there is much probability in the view entertained by Owen—namely, that some of them were simply covered by callous integument."

As regards the mental powers, Professor Marsh remarks: "The brain-cavity of *Uintatherium* is perhaps the most remarkable feature in this remarkable genus. It proves conclusively that the brain (fig. 1262, A) was proportionately smaller than in any other known mammal, recent or fossil, and even less than in some reptiles. It is, in fact, the most reptilian brain in any known mammal. In *U. mirabile* the entire brain was actually so diminutive that it could apparently have been drawn through the neural canal of all the presacral vertebræ, and certainly through the cervicals and lumbars."

Suborder 7. Proboscidea. — The last of the suborders into which the Ungulates are divided is that of the Proboscidea, represented at the present day solely by the two species of Elephant, but in past epochs including a large number of more or less closely allied forms. These animals are of huge bulk and stout build, and

include the largest known mammals. They present the following characteristic features; those of the soft parts being, of course, only known in the existing species. The nose is produced into a long flexible proboscis terminated by the nostrils (fig. 1264); from which feature the name of the suborder is derived. The limbs are stout, with their segments placed nearly in a vertical line (fig. 1267), and the proximal segment the longer. In the second segment the two component bones (radius and ulna in the fore, and tibia and fibula

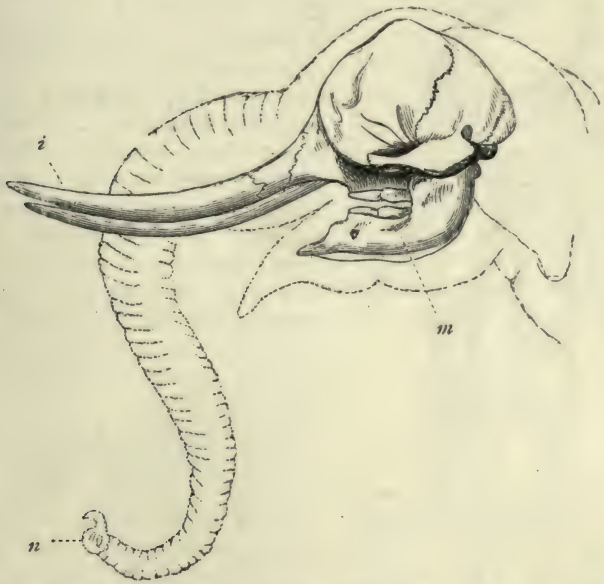


Fig. 1264.—Skull of the Indian Elephant (*Elephas indicus*). Greatly reduced. *i*, Tusk-like upper incisors; *m*, Lower jaw; *n*, Nostrils, placed at the end of the proboscis.

in the hind limb) are distinct. In the carpus the scaphoid is supported by the trapezoid, but not by the magnum, the latter supporting the lunar; while in the tarsus the cuboid articulates proximally with the distal face of the navicular, but not with the astragalus. In both the carpus and tarsus the component bones interlock but very slightly; the type of structure of the tarsus being one step in advance of that obtaining in the Condylarthra. The feet (fig. 1265) are plantigrade; there are five digits to each foot; the astragalus (fig. 1265) is flat; the femur has no third trochanter; the fibula articulates with the calcaneum; and the jugal forms the middle of the zygomatic arch. The brain is of large size; canines appear to be always absent; while incisors, growing from persist-

ent pulps, are present either in the upper or lower jaws of the males of all the forms at present known. The cheek-teeth may attain extreme complexity; and the true molars always consist of transverse ridges, which may vary greatly in height, and may be either uninterrupted, or split up into inner and outer columns, which may have a more or less alternate arrangement; there are never fewer than three such ridges in the last milk and the first true molars; and the intervening valleys may be either entirely open, or blocked by accessory tubercles, or completely filled with cement. The toes are all invested in a common integument, although furnished with distinct broad hoofs; and the third digit of each foot is the largest. There are two anterior venæ cavæ entering the right auricle of the heart; the stomach is simple; there is a large cæcum; the testes are permanently retained in the abdomen; the uterus has two cornua; and the placenta is non-deciduate and zonary.

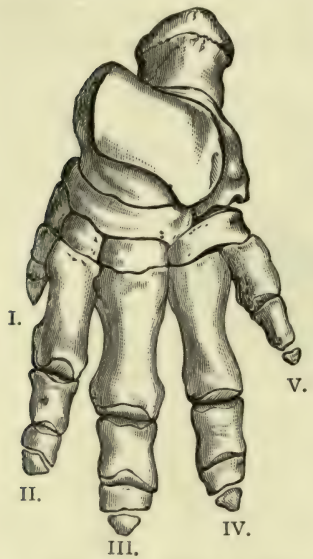


Fig. 1265.—Dorsal aspect of the left pes of the Indian Elephant (*Elephas indicus*). Greatly reduced. (After Cuvier.) The numbers indicate the digits. The uppermost bone is the calcaneum, resting upon which is the astragalus, with its flat tibial surface. The bone with a long narrow dorsal surface immediately below the astragalus is the navicular; while the one supporting the metatarsals of the fourth and fifth digits is the cuboid.

In the skull and dentition the members of this suborder are decidedly specialised; but in other respects, such as the structure of the limbs, and the presence of two venæ cavæ, they show very generalised features; and there are not wanting indications of a remote affinity with the Rodents, and perhaps the Sirenia. It will be shown as we proceed that the structure of the cheek-dentition has advanced from a comparatively generalised type in *Dinotherium* to an extremely specialised one in the existing species of Elephants; and it appears that this specialisation "has followed to a considerable extent a line analogous to that obtaining in the Perissodactyla and Artiodactyla, and shows itself in the increased height and complexity of the crowns of these teeth and in the final attainment of a nearly horizontal and continuous plane of wear. From the structure of the cheek-teeth in the more generalised members of the suborder, it may be inferred that the action of the molars of one jaw upon those of the other must have been mainly a scissor-like or snapping

one, while in the more specialised forms this action has been converted into a perfect grinding motion."[1]

The pelvis of the Proboscidea is characterised by the vertical position and great expansion of the large ilia, and the very small size of the ischia and pubes, both of which enter into the formation of the very short symphysis.

The Proboscidea make their first appearance in the Middle Miocene (Sansan stage) of Europe; but we are still unacquainted with any form which connects them decidedly with the other suborders of the Ungulata, although *Dinotherium* affords an inkling of how such a transition may have taken place. The Mastodons probably originated in Europe, from whence they travelled to India, and there gave origin to the peculiar Stegodont group of Elephants, which are the parents of the existing specialised forms. From the eastern regions of the Old World it seems probable that the higher Elephants travelled back to Europe, while they also reached North America in the Pleistocene epoch; Mastodons having arrived in the New World during the preceding Pliocene period.

Family Dinotheriidæ.—This family is at present known solely by the genus *Dinotherium*, of which the remains are found in the

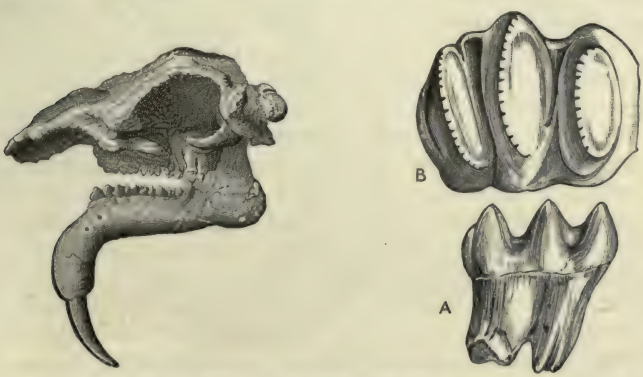


Fig. 1266.—Skull, and lateral (A) and oral (B) aspects of the first lower true molar of *Dinotherium giganteum*; from the Upper Tertiary of Europe. All the figures are reduced; the reduction of B being less than that of A.

Miocene and Pliocene of Europe and India. The type species is *D. giganteum* (fig. 1266), originally described by Cuvier, upon the evidence of a molar tooth from the Middle Miocene of the Orleannais, as a gigantic Tapir, but better known by the cranium and

[1] Quoted from the writer's 'Catalogue of Fossil Mammalia in the British Museum,' pt. iv., from which other extracts have already been made.

jaws obtained by Drs Kaup and Klipstein from the Lower Pliocene of Eppelsheim, in Hessen-Darmstadt. *Dinotherium* was an animal of the bulk of an Elephant, characterised by the presence of a pair of tusk-like, backwardly-curved incisors in the lower jaw, and by having in the adult five cheek-teeth, of which the two first are premolars. The true molars carry simple, low, transverse ridges; of which there are three in the first tooth of the series (fig. 1266, A, B), and two in each of the others. The upper premolars differ from the true molars in having their two transverse ridges connected on the outer side by a longitudinal ridge, which causes these teeth to be of the lophodont type of those of the Tapirs. In the young animal there were three milk-molars in each jaw, which resemble the true molars in structure; each of the first two having a pair of transverse ridges, while the third has three of these ridges, and thus resembles the first true molar. The number of ridges in the milk and true molars may therefore be represented by the ciphers *Mm.* $\frac{2 \cdot 2 \cdot 3}{2 \cdot 2 \cdot 3}$, *M.* $\frac{3 \cdot 2 \cdot 2}{3 \cdot 2 \cdot 2}$; the import of which we shall notice under the head of the *Elephantidæ*. *Dinotherium indicum*, from the Upper Miocene and the Lower Pliocene of North-western India, was probably nearly allied to the European species.

Family Elephantidæ.—With this family we enter a group of animals in which the succession of the cheek-teeth presents such marked peculiarities as to require special notice at the outset. In the existing members there are normally six of such teeth, which increase gradually in size and complexity from the first to the last. The last three of these teeth correspond to the true molars of less aberrant Ungulates, while the anterior ones represent the last three milk-molars of the same. These milk-teeth are not succeeded by premolars, but the whole series of teeth is gradually pushed forwards in the jaw; the anterior teeth being worn away and their roots absorbed before the hinder ones come into use. In consequence of this arrangement, and the large absolute size of the teeth, there are never more than portions of two cheek-teeth on either side of each jaw in use at any one time, as is shown in fig. 1264. The cheek-teeth of the existing Elephants will therefore correspond to *Mm.* 2 + *Mm.* 3 + *Mm.* 4 + *M.* 1 + *M.* 2 + *M.* 3 of the typical series, but it is not improbable that in very rare instances *Mm.* 1 may also be developed. If we had to depend entirely on the evidence of the existing forms, there might be some doubt as to the serial homology of the three teeth which we reckon as milk-molars; but this question is set at rest by some of the fossil forms, in which these teeth were vertically succeeded by small, and usually functionless, premolars. The total disappearance of the premolars, and the persistence of the milk-molars in the higher forms, is the widest departure from

the simple marsupial dentition known in the whole class. In some of those fossil forms in which the structure of the cheek-teeth is simpler, there may be portions of three such teeth in use at the same time. The serial position of individual teeth in any one species can be more or less exactly determined by their absolute size, and the number of transverse ridges which they carry. In all members of the family there are never less than three ridges in the fourth milk-molar and the first and second true molars (which are often collectively spoken of as the "intermediate molars"), while the last true molar has one or more ridges in excess of the preceding tooth. Incisors are always present in the upper jaw of male individuals, and may or may not be also developed in the lower jaw. In transverse section the dentine of these teeth displays a peculiar arrangement of decussating lines, similar to the "engine-turning" on the back of a watch-case, by the presence of which true ivory can always be recognised.

The earliest and least specialised genus of this family is *Mastodon*,[1] in which premolars and lower incisors are frequently present, and

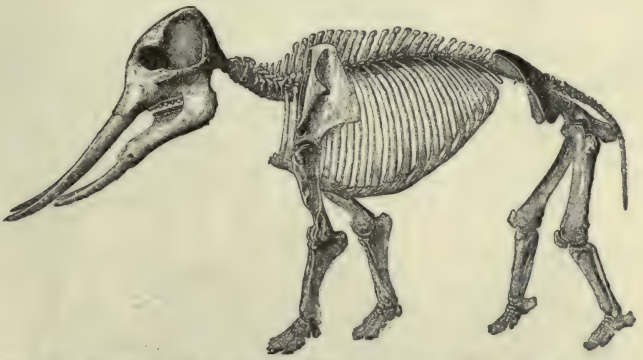


Fig. 1267.—Restoration of the skeleton of *Mastodon angustidens*. Greatly reduced. (After Gaudry.)

the upper incisors may have longitudinal bands of enamel. The cheek-teeth carry transverse ridges, which may be entire or may be divided into distinct inner and outer columns with a more or less

[1] Professor Cope proposes an arrangement of the *Elephantidæ* differing from the one generally adopted. Thus the genus *Mastodon* is split up into *Tetrabelodon*, in which there are both upper and lower tusks, and the former have an enamel-band; *Dibelodon*, in which the lower tusks are usually wanting, but the upper ones have an enamel-band; and *Mastodon*, in which there are no lower tusks, and no enamel-band on the upper ones. *Elephas* is divided into *Emmenodon*, typically represented by *Elephas Clifti* (apparently the type of *Stegodon*), but also including *E. planifrons*, and characterised by the presence of premolars; and *Elephas*, which is taken to include all the other species.

alternate arrangement; outlying tubercles may be present in the intervening valleys, which are frequently entirely devoid of cement, and are never completely filled by it. All the "intermediate" molars usually have the same number of ridges; this number varying from three to five. The ridges are always bisected by a median cleft traversing the long axis of the crown; and the plane of wear of the crowns of the teeth is oblique, that of the upper jaw inclining from

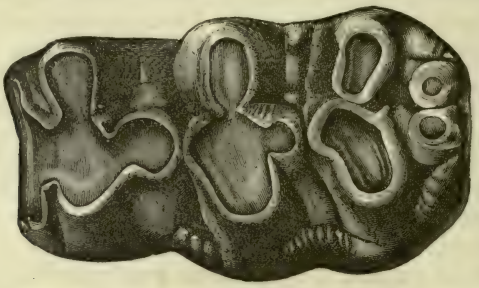


Fig. 1268.—*Mastodon angustidens.* The fourth left lower milk-molar; from the Lower Siwaliks of India.

the outer to the inner side, and the reverse obtaining in the lower. Three cheek-teeth may be in use at the same time, and the symphysis of the mandible may be greatly elongated. The vertex of the cranium (fig. 1267) is usually but slightly elevated, as in the majority of Ungulates; and in the less specialised forms (as may be seen by comparing fig. 1267 with fig. 1270) the proportions of the

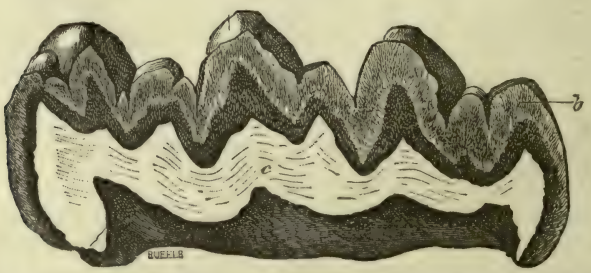


Fig. 1269.—*Mastodon angustidens.* Vertical longitudinal section of the first lower true molar; from the Middle Miocene of France. Two-thirds natural size. *b*, Enamel; *c*, Dentine. (After Gaudry.)

entire skeleton depart less widely from the same type. The genus has been divided into two groups, according to the number of ridges in the cheek-teeth. In the first or *Trilophodont* group, the number of complete ridges in each of the three "intermediate" molars is three (fig. 1268); the ridge-formula of the complete series of cheek-

teeth being represented by the ciphers *Mm.* $\frac{1 \cdot 2 \cdot 3}{1 \cdot 2 \cdot 3}$, *M.* $\frac{3 \cdot 3 \cdot 4}{3 \cdot 3 \cdot 4}$. It will be noticed that in this section the number of ridges in the third and fourth milk-molars and the first true molar is the same as in *Dinotherium*.

One of the earliest examples of this group is *M. angustidens* from the higher Miocene of both Europe and India, of which two lower cheek-teeth are represented in plan and section in figs. 1268 and 1269. The simple structure of these teeth is shown in the section, where the valleys separating the low, interrupted ridges, are seen to be devoid of cement, although partially blocked by outlying tubercles. The imperfect fourth ridge at the hinder extremity (right side of figures) of these teeth is termed the *talon*. The mandibular symphysis (fig. 1267) in this species was elongated and furnished with a pair of incisors; while the milk-molars were succeeded by premolars. Allied to this species are *M. pandionis* of the Upper Miocene and Pliocene of India, and *M. pentelici* of

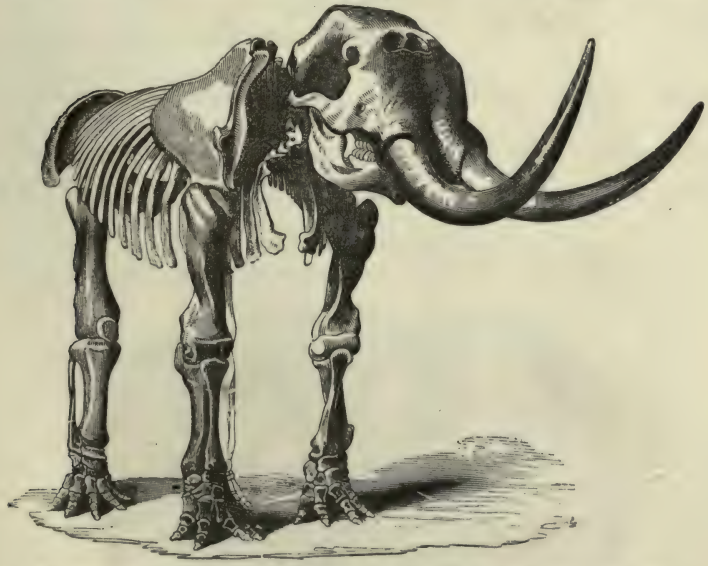


Fig. 1270.—Skeleton of *Mastodon americanus*; from the Pleistocene of Missouri. Much reduced.

the Lower Pliocene of Attica, Hungary, Samos, and Persia. From *M. angustidens* there is but a step to the contemporaneous European *M. turicensis*, in which the ridges of the molars extend straight across their crowns, without outlying tubercles in the valleys; and from this species, again, the transition is easy to the Pliocene *M. Borsoni* of Europe, in which the mandibular symphysis has become shortened in consequence of the absence of lower incisors. A later offshoot from the same branch is found in *M. americanus* (frequently known as *M. giganteus*,

or *ohioticus*) of the Pleistocene of North America. Remains of this species (figs. 1270, 1271) are exceedingly abundant in the celebrated "Big-Bone-Lick" of Kentucky, in which region the species survived into the human period. Although the mandibular symphysis is short, a single small incisor is occasionally found on one side of the jaw; premolars had however disappeared.[1] Other Trilophodont species are *M. Humboldti* and *M. cordillerum* (*andium*) of the Pleistocene of South America, in both of which the transverse ridges of the cheek-teeth are broken into columns. The former species is distinguished by the short and edentulous symphysis of the mandible. According to Dr Falconer, the latter had an elongated mandibular symphysis and large lower incisors; but Dr Burmeister states that this reference is incorrect, and that the symphysis was short and tuskless.

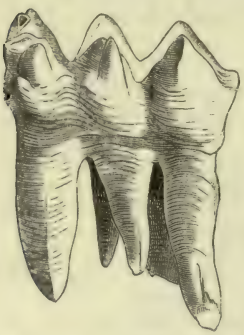


Fig. 1271.—Outer view of second left lower true molar of *Mastodon americanus*. Reduced.

In the *Tetralophodont* group the number of ridges in the cheek-teeth is greater than in the former group, there being usually four in the "intermediate" and five in the last true molars; but there may be occasionally five in the former and six in the latter. The complete normal ridge-formula is, therefore, *Mm.* $\frac{2-3-4}{2-3-4}$, *M.* $\frac{4-4-5}{4-4-5}$.

In this group *Mastodon arvernensis*, from the Upper Pliocene of Europe, is characterised by the number of accessory tubercles on the

Fig. 1272.—*Mastodon arvernensis*; the fourth left upper milk-molar; from the Norwich Crag. (After Lyell.)

crowns of the cheek-teeth (fig. 1272) and the somewhat alternate arrangement of the inner and outer columns of their transverse ridges, by which

[1] It appears probable that these teeth may occasionally be developed as an abnormality.

means the transverse valleys become more or less completely blocked. Closely allied to this species is *Mastodon sivalensis*, of the Pliocene of Northern India, of which a last upper true molar is represented from the lateral aspect in fig. 1273; in this species there are occasionally five

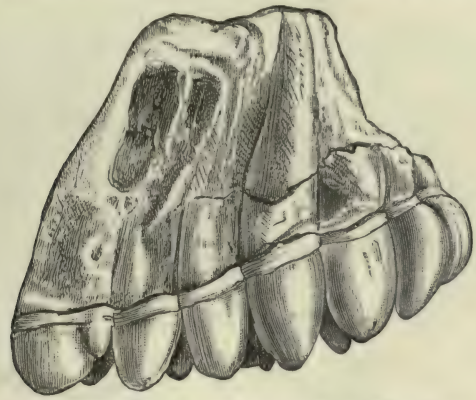


Fig. 1273.—Profile view of last upper true molar of *Mastodon sivalensis*; from the Pliocene of the Siwalik Hills of India. Reduced.

ridges in the "intermediate" molars, and the last upper true molar (as in the figure) may have six ridges and a hind talon; the blocking of the valleys by the alternate arrangement of the inner and outer columns of the ridges is well exhibited in the woodcut. Both in this species and *M. arvernensis* the symphysis of the mandible is short and tuskless, as in the modern Elephants; and the Siwalik species is further characterised by the great elevation of the vertex of the skull (fig. 1274), in which respect it also agrees with the last-named group. Both these species must be regarded as highly specialised forms which have diverged from the line connecting the *Trilophodont* group with the true Elephants. We may here briefly mention *M. perimensis* and *M. punjabiensis* of the Indian Pliocene, which show certain characters intermediate between the two above-mentioned species and *M. longirostris*, which we now proceed to notice. The last-named species occurs typically in the Lower Pliocene bone-sand of Eppelsheim in Hessen-Darmstadt, but has been also found in the English Red-Crag. It has an elongated mandibular symphysis furnished with a pair of short incisors (fig. 1275), and

Fig. 1274.—Left lateral view of the skull of *Mastodon sivalensis*; from the Siwalik Hills of India. Greatly reduced. (After Falconer and Cautley.)

the ridges of the cheek-teeth (fig. 1276) are nearly straight, and the intervening valleys only partially blocked by tubercles. The latter woodcut shows the progressive increase in the number of ridges of the milk-molars of the present group; the first and second true molars, which

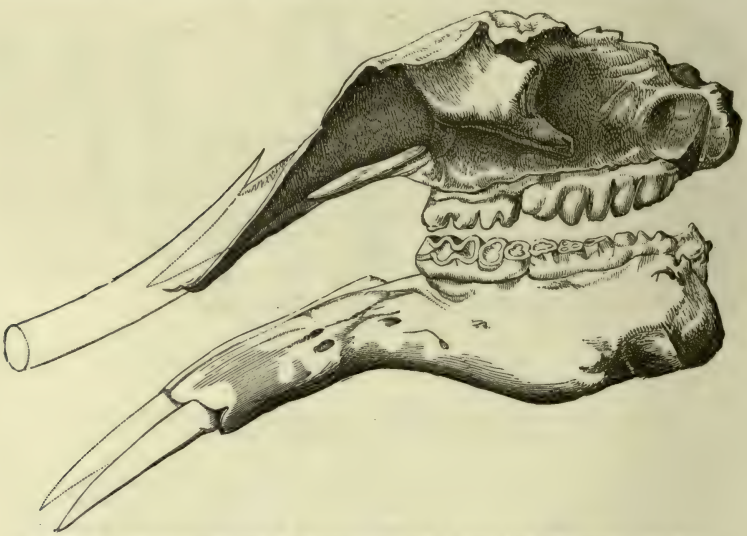


Fig. 1275.—Left lateral view of the imperfect skull of *Mastodon longirostris*; from the Bone-sand of Hessen-Darmstadt. Much reduced. (After Kaup.)

would follow the fourth milk-molar (the right-hand tooth in the figure), each have the same number of ridges as the latter. *M. Cautleyi*, of the Pliocene of Western India, is a form connecting the last species with *M. latidens*. The latter is very widely distributed, ranging in the Pliocene

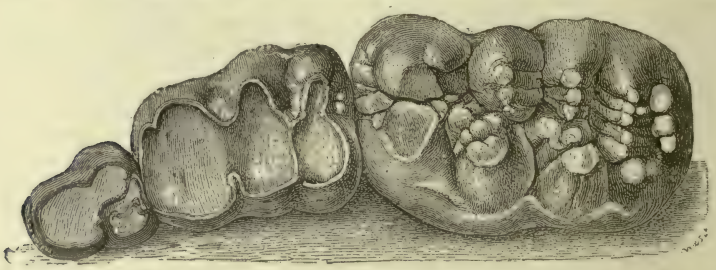


Fig. 1276.—The three left upper milk-molars of *Mastodon longirostris*; from the Bone-sand of Hessen-Darmstadt. (After Kaup.)

from India and Burma to Borneo; the symphysis of the mandible is short; the molars (fig. 1277) are very wide, with their ridges and valleys straight and uninterrupted; and these teeth pass so completely into the type of those of the least specialised species of *Elephas* as to indicate

that there is really no distinction between that genus and *Mastodon*, although the retention of the latter term for the more generalised forms of what would be otherwise a very unwieldy genus is convenient.

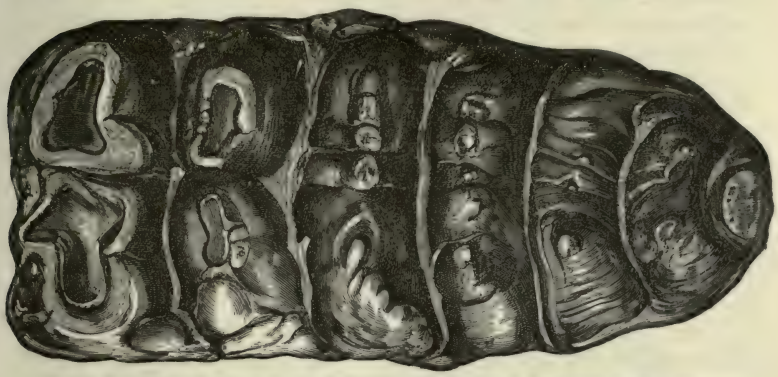


Fig. 1277.—Crown surface of the third left upper true molar of *Mastodon latidens*; from the Pliocene of Borneo. Two-thirds natural size.

With the above-mentioned proviso as to its apparent passage into *Mastodon* we may note the chief features of the existing genus *Elephas*.

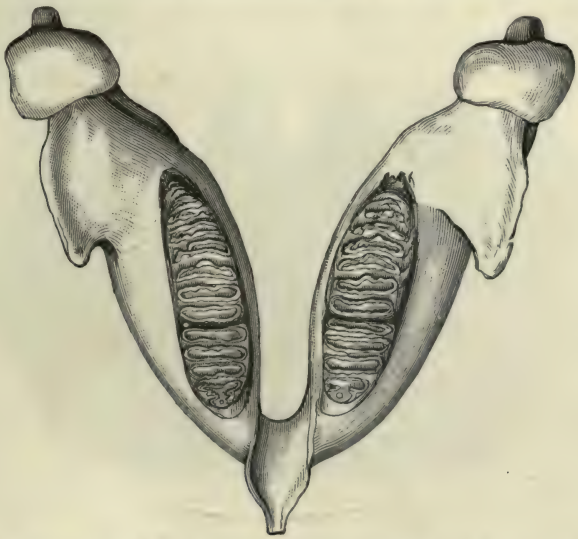


Fig. 1278.—Palatal view of the mandible of the Indian Elephant (*Elephas indicus*). Greatly reduced. The hinder portion of the penultimate and the anterior half of the last true molars are in use.

Thus lower incisors (tusks) are invariably wanting; the enamel on the upper incisors merely forms a small cap at their extremities;

premolars are nearly always absent; while the mandibular symphysis is never produced into a long rostrum, but usually terminates in a short spout-like channel, as in fig. 1278. The ridges of the true molars extend straight across their crowns, and generally show no sign of division into inner and outer columns; there is always a certain quantity of cement in the valleys between the ridges; and in those species in which these ridges become developed into tall thin plates, the cement forms equally tall laminæ filling the intervening spaces. In the least specialised forms the number of the ridges in the "intermediate" molars may be as low as five; while those in the last true molar may vary from seven in the least specialised to upwards of twenty-four in the most specialised species. Finally, it is only in a few of the more generalised species that the "intermediate" molars have an isomerous ridge-formula.

Like the Mastodons, this genus is divided into two groups, according to the structure of the teeth. In the first, or *Stegodont*, group, which is entirely confined to the Eastern parts of the Old World, the number of ridges in the cheek-teeth is comparatively low, and there may be only five or six of such ridges in the "intermediate," and from seven to eleven in the last upper true molars.

The structure of the molars of *Elephas Clifti*, from the Pliocene of India, Burma, and Japan, which is the most generalised species of the

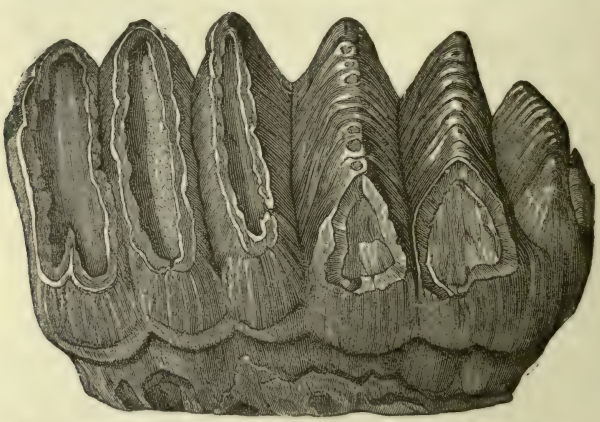


Fig. 1279.—*Elephas Clifti*. The first left upper true molar; from Burma. One-half natural size. (After Clift.)

genus, is shown in fig. 1279; where it will be seen that the ridges are low and roof-like, and that the cement is confined to the bottom of the intervening valleys. The molars of this species (in which premolars were developed), it will be seen, are but one step in advance of those of the Tetralophodont Mastodons. In other species of this group, like *E. in-*

signis, the ridges of the molars (fig. 1280[1]) become more numerous, and somewhat higher; while the intervening valleys are more or less completely filled with cement. The number of ridges in the cheek-teeth of this species may be represented by the formula $Mm.\ \frac{2.(5-6).7}{2.5.(7-9)}$, $M.\ \frac{(7-8).(7-8).(9-11)}{(7-10).(8-12).(9-13)}$. Allied species are *E. bombifrons* and *E. ganesa*, which are found in the Pliocene of India and the countries to the eastward as far as Japan.

In the second, or *Elephantine*, group, the specialisation of the molars becomes greater; in all the species the ridges are so tall that they assume the appearance of plates, but there is great varia-

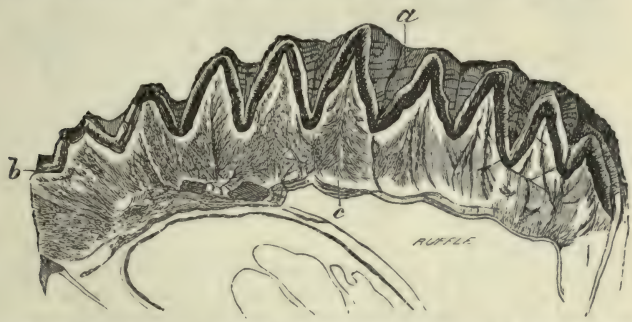


Fig. 1280.—*Elephas insignis*. Vertical and longitudinal section of the third left upper true molar; from the Pliocene of the Siwalik Hills. One-third natural size. *a*, Cement; *b*, Enamel; *c*, Dentine. (After Falconer and Cautley.)

tion in respect to their height and number; those of the less specialised forms not being more numerous than in *E. insignis*. The cement always completely fills the interspaces between the ridges, and in the higher forms these interspaces are extremely narrow.

One of the least specialised members of this group is *Elephas planifrons*, from the Pliocene of Northern India, of which the section of an upper molar is represented in fig. 1281. In the teeth of this species the number of the ridges is nearly the same as in *E. insignis;* but, as will be seen from the figure, the ridges have become much taller and thinner, and the valleys are completely filled up with cement. It results from this structure that when the crown of the tooth has become well worn (as in the anterior half of fig. 1282), its grinding aspect will present a nearly flat surface marked by a series of transversely elongated raised disks of enamel, each enclosing an islet of dentine. This structure, which is still better exemplified in the more-worn molar of the closely allied *E. meridionalis* (fig. 1283), of the Upper Pliocene of Tuscany and the Norfolk "Forest-bed," is admirably adapted for the attrition of vegetable matter owing to the inequalities produced on the surface, due to the variation in

[1] In this figure, as well as in fig. 1281, the tooth is turned the wrong way upwards.

the density of the different layers of which the tooth is composed. The enamel-disks of both the species under consideration are, when partially worn, generally expanded in the middle, and are often interrupted in their course across the crown; in the European species the enamel itself being thrown into a series of fine plications, or crenulations. Both *E. meridionalis* and *E. planifrons* attained gigantic dimensions, the height

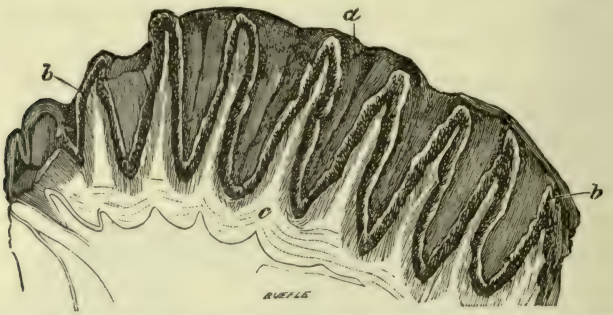


Fig. 1281.—*Elephas planifrons*. Vertical and longitudinal section of the second upper true molar; from the Pliocene of the Siwalik Hills. One-third natural size. Letters as in fig. 1280. (After Falconer and Cautley.)

of some individuals of the former being estimated at upwards of fifteen feet, while a fair average height of males of the existing Indian species is not greater than nine feet. *E. planifrons* is remarkable as being the only member of the Elephantine group in which premolars were developed. Somewhat more specialised, both in regard to the height and number of the ridges of the cheek-teeth, and also in the elevation of the vertex of the cranium, is *E. hysudricus*, of the Pliocene Siwaliks of India, which may perhaps have been the ancestor of the existing species of

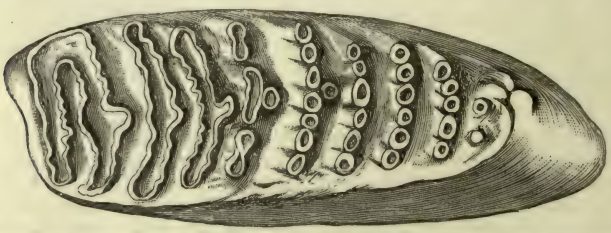


Fig. 1282.—Grinding surface of upper molar of *Elephas planifrons*, one-third natural size; from the Pliocene of India. (After Falconer and Cautley.)

that country. In *E. antiquus*, of the Pleistocene of Europe, we have a species with the ridges of the cheek-teeth somewhat more numerous than in the last form, although less so than in *E. primigenius*; their number being represented by the formula $Mm.\ \frac{(2-3).(5-7).(8-11)}{3\ .(6-8).(9-11}$ $M.\ \frac{(9-12)\ .(12-13).(15-20)}{(11-12).(12-13).(16-21)}$. The molars (fig. 1284) are usually relatively narrow, and there is very generally (especially in the lower jaw)

median expansion of the worn enamel-disks of the ridges, which thus approach a lozenge-shape. The range of this species in England does not extend northwards of Yorkshire, and it goes as far south as Algeria,

Fig. 1283.—Upper molar of *Elephas meridionalis*, one-third natural size; from the Upper Pliocene of Tuscany.[1]

where the allied *E. atlanticus* is also found. From the molars of *E. antiquus* there is but a step to those of the existing African Elephant (fig. 1285), in which the enamel-disks assume a still more decided lozenge-

Fig. 1284.—The second right lower true molar of *Elephas antiquus;* from the Pleistocene of England. One-third natural size.

shape; and the small *E. mnaidriensis* and *E. melitensis*, of the Pleistocene cavern and fissure-deposits of the Maltese and neighbouring islands, are more or less closely allied forms. The height of the smallest indi-

Fig. 1285.—A right upper true molar of *Elephas africanus;* Recent. Africa. One-third natural size.

viduals of the last-named, or "Pigmy Elephant," is estimated as not greater than three feet. Another peculiar Elephant is *E. namadicus*, from the Pleistocene of the Narbada Valley, in Western India, and Japan,

[1] The hinder part of this tooth is to the left; the position of the preceding figure being the reverse.

which is closely allied in dental characters to *E. antiquus*, although distinguished by a very prominent overhanging ridge on the frontals. Here we may also mention *E. Columbi*, of the Pleistocene of Central and North America, and *E. armeniacus* from Armenia; the former being intermediate in the structure of its teeth between *E. antiquus* and *E. indicus*, and the latter between *E. primigenius* and *E. indicus*. It is, however, not improbable that *E. Columbi* is only a variety of the Mammoth. Lastly,

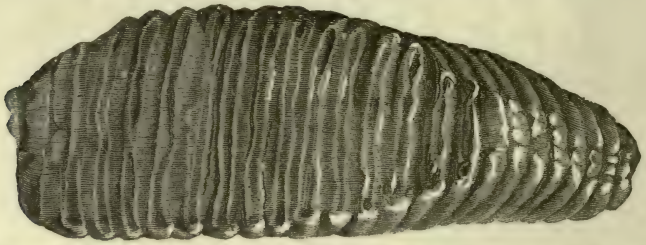


Fig. 1286.—A half-worn third left upper true molar of the Mammoth (*Elephas primigenius*), viewed from the grinding surface; from the Pleistocene of Europe. One-third natural size.

we have the Mammoth (*E. primigenius*), in which the number of ridges in the molars is represented by the high figures *Mm.* $\frac{(3\text{–}4)\,.\,(6\text{–}9)\,.\,(9\text{–}12)}{(3\text{–}4)\,.\,(6\text{–}9)\,.\,(9\text{–}12)}$, *M.* $\frac{(9\text{–}15)\,.\,(14\text{–}16)\,.\,(18\text{–}27)}{(9\text{–}15)\,.\,(14\text{–}16)\,.\,(18\text{–}27)}$. "The incisors are usually long, spiral, and not very thick near the alveolus; they are, however, subject to great variation. The molars (fig. 1286) are relatively wide in proportion to their length; their ridges are narrow and closely packed, with the cement, enamel, and dentine very thin; the plication of the enamel is usually slight; the worn dentine-disks are very narrow; and the crown is usually characterised by the extreme flatness of its wear. Variations are common, and those molars in which the ridges are thicker and less numerous, and the enamel is more plicated, approach very closely to certain examples of *E. antiquus*. The existing Indian species presents a close approach in dental and skeletal structure, but the molars are decidedly of a less specialised type, and thereby indicate that the living species is not a descendant of the Mammoth." This animal was covered with a thick woolly coat, and also with an outer covering of long hair, by which means it was protected from the climatal rigours of the northerly regions over which it once roamed. Remains of the Mammoth have been found in Northern Europe, Asia, and America; and in the frozen soil of the banks of the Siberian rivers numerous carcasses have been

Fig. 1287.—Lateral view of a half-worn upper true molar of the Mammoth. About one-third natural size.

found with the dried flesh, skin, and hair preserved; the skeleton of one of these specimens, with portions of the skin still adhering to it, being preserved in the Museum at St Petersburg (fig. 1288). The Mammoth was essentially northern in its distribution, apparently not passing southwards of a line drawn through the Pyrenees, Alps, the

Fig. 1288.—Skeleton of the Mammoth. Greatly reduced. Portions of the integument still adhere to the head, and the thick skin of the soles is still attached to the feet.

northern shores of the Caspian, Lake Baikal, Kamschatka, and the Stanovi Mountains. Its remains occur in the Norfolk "Forest-bed," and from this date the species existed right through the glacial epoch, and was well known to the primitive human inhabitants of Northern Europe, as is testified by its portrait drawn on a fragment of its own tusk by one of these early hunters.

Finally, it should be mentioned that a portion of a tusk of a Proboscidean, said to have been obtained from the Pleistocene of Australia, has been described as *Notelephas*. There are, however, no characters in this specimen to indicate its right to generic distinction, and its reputed origin must be looked upon with great suspicion.

Group Tillodontia.—Here may be noticed a remarkable group of Mammals from the Lower Eocene, of which the position is still unsettled. They are regarded by Professor Marsh as constituting a distinct order; while Professor Cope subdivides them into Tillodontia and Tæniodontia, and includes them in his order Bunotheria. A suggestion has also been made of affinity with the Edentates. These Mammals, as will be gathered from the characters mentioned below, present certain characters common to the Ungulata, Rodentia, and Carnivora, but to include them in either one of those orders would render it impossible to give anything approaching to a definition of the order so enriched. Putting aside the suggestion of Edentate affinities as requiring further evidence, the characters presented by the Tillodonts harmonise with the view that both the Ungulates and Rodents have been derived from a primitive Carnivorous stock.

Family Anchippodontidæ.—The genus *Anchippodus* (*Trogosus*), with which *Tillotherium* (fig. 1289) is closely allied or identical, is

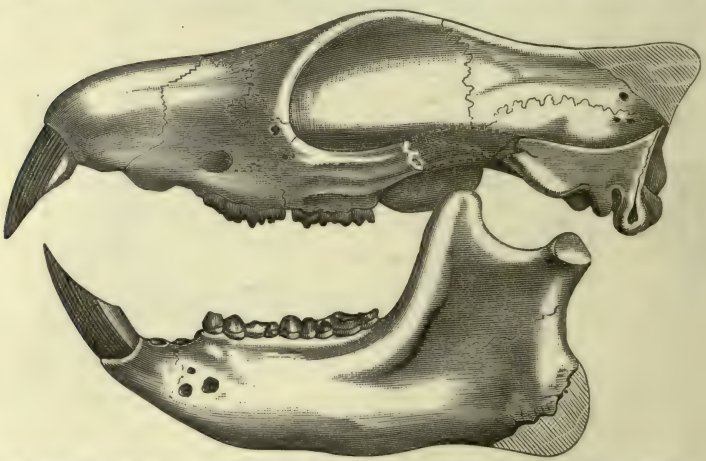


Fig. 1289.—Left lateral aspect of the skull of *Tillotherium fodiens*; from the Lower Eocene of North America. One-fourth natural size. (After Marsh.)

from the Lower Eocene of North America, and apparently has the dental formula $I.\frac{2}{2}$, $C.\frac{1}{1}$, $Pm.\frac{3}{4}$, $M.\frac{3}{3}$. The lower cheek-teeth

resemble those of *Palæotherium*, but the upper true molars are of the triangular tritubercular type. The first pair of incisors is small, but the second is large and scalpriform, with persistent pulps like the incisors of the Rodents. In many respects the skeleton approximates to that of the Creodonta; the femur has a third trochanter; the feet were five-toed, with the whole sole applied to the ground, and having ungual phalanges similar to those of the Bears. The brain-cavity is of small size, and the cerebral hemispheres did not extend over the cerebellum or the olfactory lobes. The orbits are not complete, but open into the temporal fossæ. Clavicles were probably present.

Family Platychœropidæ.—The type genus of this family is *Platychœrops* (*Miolophus*), from the London Clay, to which the

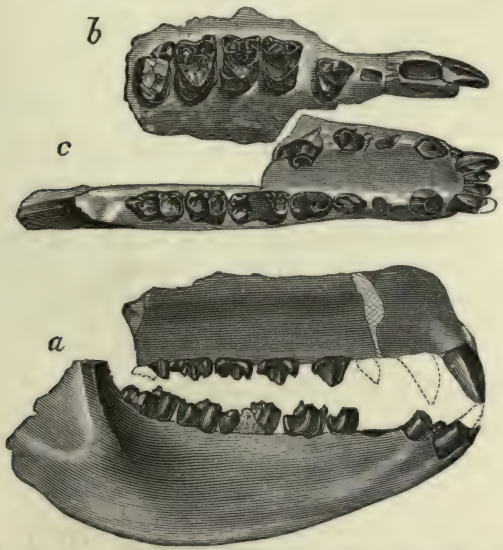


Fig. 1290.—*Esthonyx Burmeisteri*.—The palate and mandible; from the Wasatch Eocene of Wyoming, U.S.A. Two-thirds natural size. *a*, Lateral view of part of cranium and mandible; *b*, Oral view of right half of palate; *c*, Oral view of mandible. (After Cope.)

North American *Esthonyx* (fig. 1290) appears to be allied. In the latter the first upper and the second lower incisors are scalpriform, but do not grow from persistent pulps; the dental formula is $I.\frac{2}{3}$, $C.\frac{1}{1}$, $Pm.\frac{3}{3}$, $M.\frac{3}{3}$ If *Esthonyx* be not allied to *Platychœrops*, the former must constitute the type of a family, which should be known as the *Esthonychidæ*. The genus *Psittacotherium*, of which the family position is uncertain, has the mandible of great

depth, and the lower molars with transverse ridges; both the first and second lower incisors being scalpriform, and growing from persistent pulps; and the genus may be regarded as connecting *Anchippodus* with *Calamodon*. The lower dental formula appears to be *I.* 2, *C.* 1, *Pm.* 3, *M.* 3; and two species are known from the Puerco, or lowest, Eocene of New Mexico.

Family Calamodontidæ.—In *Calamodon*, the type genus of this family (the Tæniodontia of Professor Cope), the lower jaw resembles that of *Psittacotherium;* there are three lower incisors, of which the second and third are scalpriform, and have their anterior surfaces faced with enamel; and the cheek-teeth are five in number, but cannot be differentiated into premolars and true molars. There is no diastema, and the cheek-teeth approximate to those of the Rodents in their massive squared crowns, and have also been considered to show resemblances to those of the Edentates. The second lower incisor is much larger than either of the others, and the mandibular condyle is transversely elongated. Professor Cope, as will be noticed below, regards this group, and more especially *Psittacotherium*, as close to the ancestral types of the Rodentia, and has also suggested their alliance to the ancestors of the Edentates; *Calamodon* is from the Wasatch or Middle Eocene.

Family Stylinodontidæ.—Professor Marsh has proposed this family name for the North American Tertiary genus *Stylinodon*, in which the molars grew from persistent pulps like those of the Edentates.

CHAPTER LXII.

CLASS MAMMALIA—continued.

Orders Rodentia and Carnivora.

Order VII. Rodentia.—The Rodents form one of the best-defined orders of the whole class, and are readily characterised by the absence of canines, and their chisel-like (scalpriform) incisors (of which there is only a single lower pair), separated by a long diastema from the cheek-teeth (fig. 1298), and of which generally only the anterior face is coated with enamel. The dentition is diphyodont and heterodont; the incisors grow from persistent pulps, and the cheek-teeth may be either rooted or rootless. The crowns of the latter are entirely adapted for grinding, and are very frequently (fig. 1292) complicated by deep infoldings of enamel. The premolars are very generally either $\frac{1}{1}$ or $\frac{0}{0}$, and the true molars $\frac{3}{3}$. The premaxillæ are large; the zygomatic arch is complete, the middle portion being generally formed by the jugal; the orbit is confluent with the temporal fossa; there is a long diastema; and the condyle of the mandible is antero-posteriorly elongated, and, through the absence of a postglenoid process in the cranium, capable of a backwards and forwards motion. The feet are generally partially or entirely plantigrade, and usually furnished with five unguiculate digits. More or less complete clavicles are present, and the acromion of the scapula frequently has a long recurving process. All the existing forms are of comparatively small size, and most of them are of terrestrial habits. The feature of hypsodontism, which we have already noticed under the head of the Ungulata, attains its greatest development in this order; its final stage being the production of rootless cheek-teeth.

That the Rodents are connected in some manner with the more

generalised Ungulates is quite evident; and Professor Cope would derive them from Tillodontia, allied to *Calamodon* and *Psittacotherium*, and accordingly considers that their lower incisors and the corresponding upper ones represent the second of the three typical pairs. This view is, however, not supported by the dentition of the young of the *Leporidæ*. The *Leporidæ* show certain points of resemblance to *Typotherium* among the Toxodontia; while in the entire order distant affinities are indicated to the Proboscidea, as is shown by the characters of the teeth, the acromion of the scapula, and the position of the jugal.[1]

This order is well known from the period of the Upper Eocene (Oligocene), while *Decticadapis* apparently carries it back to the commencement of the Tertiary. It has not suffered very greatly by the extinction of family types at the present day, although all the gigantic forms have completely disappeared.

Suborder 1. Duplicidentata.—This suborder is characterised by the number of the incisors, which in the adult are $\frac{2}{1}$, but at birth $\frac{3}{1}$. The outer pair of upper incisors is very soon lost, the second pair being of small size, and placed directly behind the large first pair. The incisive palatal foramina are large and confluent; the fibula is anchylosed to the tibia, and articulates with the calcaneum. The enamel-coat of the incisors is not entirely confined to their anterior surface.

Family Leporidæ.—In this family the number of cheek-teeth is *Pm.* $\frac{3}{2}$, *M.* $\frac{3}{3}$; these teeth being rootless, with transverse enamel-folds. The clavicles are imperfect, and the fore limbs shorter than the hind ones. This family includes at the present day only the cosmopolitan genus *Lepus*, comprising the Hares and Rabbits. Existing species of that genus have left their remains in the caves of Europe and Brazil; while extinct ones are found in the Upper Pliocene of France (*L. Lacosti*), in the Siwaliks of India, and in the John Day Miocene of North America. *Palæolagus* from the Miocene of the latter country is closely allied to *Lepus;* while *Panolax* from equivalent strata in New Mexico has only a single plate in the first upper true molar.

[1] The Rodents differ from the Proboscidea in having a discoidal in place of a zonary placenta; but it has recently been found that in the Mouse there are traces of this discoidal placenta having been derived from an earlier zonary one. The zonary placenta of the Proboscidea is evidently a specialisation of the diffused placenta of the other Ungulates; and we can now see how a further specialisation of the zonary placenta results in the discoidal one of the Rodents, Insectivores, and Primates.

Family Lagomyidæ.—This family includes very small Hare-like Rodents, with short ears, complete clavicles, and the fore limbs not shorter than the hinder. They are very characteristic of the mountains of Central and Northern Asia, but also occur in those of Europe and North America. Their cheek-teeth resemble those of *Lepus*, but the premolars are never more than $\frac{2}{2}$, and may be reduced to $\frac{1}{1}$. Those extinct forms in which the premolars are $\frac{2}{1}$ have been separated from the existing genus *Lagomys* as *Myolagus*, and those with only *Pm.* $\frac{1}{1}$ as *Titanomys*, but it appears preferable to include all these variations in the type genus. The Pleistocene of Europe contains remains of some existing and some extinct (*L. sardus*) species, and the genus is well represented in the Tertiaries of the Continent as far down as the Lower Miocene (Upper Oligocene); the species of the latter horizon being *L. visenoviensis* (fig. 1291), the type of *Titanomys*. Fossil remains of this genus have also been found in the Pleistocene cave-deposits of Port Kennedy in the United States.

Fig. 1291.—Left ramus of the mandible (outer view) of *Lagomys visenoviensis*; from the Lower Miocene of Europe.

Suborder 2. Simplicidentata.—The incisors are always $\frac{1}{1}$, and have the enamel confined to their anterior surface. The incisive foramina on the palate are of moderate size; and the fibula does not articulate with the calcaneum.

Family Caviidæ.—This and the following five families compose the section *Hystricomorpha*. The *Caviidæ*, which are now exclusively confined to America, have four anterior and three posterior digits, and in the existing genera the crowns of the molars are divided by enamel-folds into transverse lobes; the number of the cheek-teeth being *Pm.* $\frac{1}{1}$, *M.* $\frac{3}{3}$. *Cavia*, in which the tail is absent, is represented by remains of several existing species in the Pleistocene of the Brazilian caves; while *Contracavia* is a much larger extinct type from the infra-Pampean of South America. *Microcavia*, again, from the Pleistocene of Argentina, presents characters connecting it with *Cavia* and the following genus. *Dolichotis* (or *Cerodon*), in which there is a short tail, is also represented in the South American Pleistocene; two species being extinct, while the third (*D. antiqua*) may be identical with the living form. Here may be provisionally placed the genera *Issiodoromys* and *Nesocerodon* from the Quercy Phosphorites and Lower Miocene of France, which

are regarded by recent authorities as related to *Dolichotis*, although formerly placed in the *Theridomyidæ*. The crowns of their molars are vertically divided by enamel-folds into two heart-shaped lobes. *Hydrochochœrus*—the largest living Rodent—is represented in the Brazilian cave-deposits by a species probably identical with the living Capybara, and also in the Pleistocene of Buenos Ayres by an extinct one estimated to have attained a length of five feet, and by a third (*H. magnus*) of still larger dimensions. An extinct species has also been obtained from the Pleistocene of South Carolina; and another from the infra-Pampean deposits of Parana. From the latter deposits other forms supposed to be more or less nearly allied to the existing genus have received the names *Cardiatherium*, *Procardiatherium*, *Cardiomys*, and *Cardiodon*; the latter name had, however, been previously applied to a Sauropodous Dinosaur,[1] and is therefore inadmissible.

Family Dasyproctidæ.—In this South and Central American family the number of the cheek-teeth is the same as in the last; and these teeth are also semi-rooted, but their crowns have external and internal enamel-folds (fig. 1292); and the incisors are long. The type genus *Dasyprocta* is represented by numerous forms in the Pleistocene of the Brazilian caves; while a *Cœlogenys* occurring in the same deposits is probably identical with the living Paca (*C. paca*).

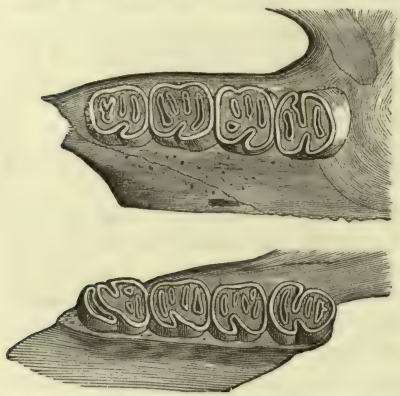


Fig. 1292.—Palatal view of the right upper and lower dentition of *Dasyprocta*. Recent. America. The tooth in each jaw on the right side of the figure is the premolar.

Family Chinchillidæ.—This third family of American Rodents has the same dental formula as the last, but the molars have continuous enamel-folds extending completely across their crowns, and the hind limbs are much elongated. The genus *Lagostomus* is represented in the South American Pleistocene by the existing Vischaca (*L. trichodactylus*), as well as by some extinct forms. *Megamys* from the infra-Pampean deposits of Patagonia and Parana is the largest representative of the order yet known; its bulk being estimated as equal to that of an Ox. Several species have been described, one of which is the type of *Potamarchus* of Dr Burmeister. Allied genera from the South American

[1] See page 1177.

deposits are *Epiblema* and *Tetrastylus;* one species of the latter having been originally referred to *Theridomys.*

Family Hystricidæ.—The Porcupines are well characterised by their spiny covering. The number of their cheek-teeth is the same as in the preceding families; and these teeth have both external and internal enamel-folds. An extinct species of the American genus *Synœtheres* occurs in the Pleistocene of the Brazilian caves, while a species of the other American genus *Erithizon* is recorded from cave-deposits in Pennsylvania. *Atherura* is found in the Pleistocene of Southern India. *Hystrix* occurs in the Pleistocene and Pliocene of India; in Europe from the Upper Pliocene of the Val d'Arno down to the Middle Miocene, and perhaps to the Quercy Phosphorites; while in North America it is represented both in the Pliocene and the White River Miocene. Finally, *Mylagaulus* from the Miocene of the United States may be allied either to *Hystrix* or *Dasyprocta* (Agouti).

Family Castoroididæ.—The gigantic *Castoroides*, of the Pleistocene of the United States, is now generally regarded as entitled to represent a distinct family although originally placed in the *Castoridæ.* Although presenting certain cranial features recalling *Castor*, its dentition comes nearest to that of *Chinchilla* and *Hydrochœrus.* The extinct genera *Loxomylus* and *Amblyrhiza*, from the Pleistocene of the Antilles, may probably be included in the same family; their dentition presenting many resemblances to that of *Chinchilla. Castoroides* must have attained the dimensions of a Bear.

Family Octodontidæ.—With the exception of *Ctenodactylus* the number of the cheek-teeth in this Ethiopian and South American family[1] is the same as in the *Hystricidæ;* these teeth having both external and internal enamel-folds, with either imperfect or perfect roots. In the South American Pleistocene we meet with existing and a few extinct species of the genus *Carterodon*, which is characterised by the broad and grooved incisors, and also of *Myopotamus* (Coypu), *Echinomys*, *Loncheres*, *Phyllomys*, and *Ctenomys.* Other forms from the South American Tertiaries allied to the latter have been named *Phloramys* and *Pithanotomys;* while *Morenia* and *Orthomys*, from the infra-Pampean beds of Parana, and *Tribodon*, from Monte Hermosa, are regarded as related to *Myopotamus.* The extinct *Pellegrinia*, from the Sicilian Pleistocene, may be allied both to the Ethiopian *Ctenodactylus* and the American *Octodon.*

Family Theridomyidæ.—This extinct family appears to be most nearly related to the preceding although connected by *Archæomys* with the *Chinchillidæ.* The cheek-teeth number $Pm. \frac{1}{1}$, $M. \frac{3}{3}$. In

1 One species of *Echinomys* occurs in Central America.

Theridomys (fig. 1293, B) they are rooted, and have three or four re-entering enamel-folds, which form isolated disks on the worn crowns. This genus occurs in the Lower Miocene and Upper Eocene of Europe; while *Syllophodus* of the North American Miocene is closely allied. *Protechinomys* of the Lower Miocene and Upper Eocene of France has rooted cheek-teeth with crowns very like those of *Theridomys* and the living *Echinomys* (*Octodontidæ*); while *Archæomys* of the same deposits has the teeth devoid of roots, with their enamel-folds continuing across the crown, and dividing it into laminæ (fig. 1293, A). *Trechomys* is a fourth allied genus from the Quercy Phosphorites, having cheek-teeth somewhat like those of *Theridomys*, but with laterally-compressed crowns.

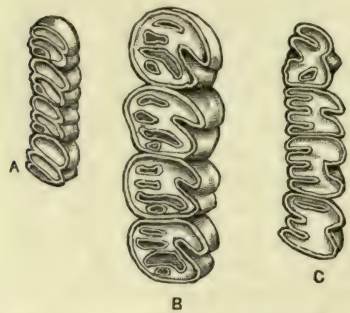


Fig. 1293.—A, Left lower cheek-teeth of *Archæomys*; B, Left upper cheek-teeth of *Theridomys*; C, Left lower cheek-teeth of *Chalicomys*. A and B enlarged. In B the uppermost, and in A and C the lowest, tooth is the premolar.

Family Dipodidæ.—This and the four following families are embraced in the section Myomorpha. In the *Dipodidæ* (Jerboas) remains of the existing *Alactaga jaculus* occur in the Pleistocene of Europe, and those of *Zapus* (*Jaculus*) *hudsonianus* in the corresponding beds of North America; while a species of *Platycercomys* has been recorded from the Pleistocene of Northern Asia. The so-called *Dipöides* of the Tertiary of Würtemberg is probably a *Chalicomys*.

Family Geomyidæ.—The American Pouched-Rats, in which the cheek-teeth are *Pm.* $\frac{1}{1}$, *M.* $\frac{3}{3}$, are represented by species of the type genus *Geomys* in the Pleistocene and Pliocene of North America, and also by one existing species of *Thomomys* in the Pliocene of Oregon. In the Miocene of the United States two extinct genera are also met with, of which *Entoptychus* is allied to *Thomomys*, and has rootless molars and broad incisors; while *Pleurolichus* has rooted molars and the incisors without grooves, like those of the allied existing genus *Heteromys*.

Family Spalacidæ.—This Old World family comprises burrowing Rodents, with large incisors, and rooted molars having re-entering enamel-folds. The only fossil representative is a *Rhizomys*, from the Siwalik Hills of India, which appears to be closely allied to the living forms; all of which are characterised by the absence of premolars.

Family Muridæ.—The *Muridæ* form by far the largest family

of the order, and are mainly characterised by certain peculiar features of the skull. With the exception of *Sminthus*, premolars are wanting; and the true molars, except in the Australian *Hydromys* and *Xeromys*, where they are reduced to $\frac{2}{2}$, are $\frac{3}{3}$ in number; while the lower incisors are laterally compressed. The molars may be rooted or rootless, and either brachydont and tuberculate, or hypsodont with re-entering enamel-folds. This family may be divided into several subfamilies. Of these the *Cricetinæ* have the cusps of the upper molars arranged in two longitudinal series; these teeth being either rooted or rootless. This subfamily, which is now the dominant one in America, but was formerly largely developed in the Old World, where it is still found, appears to represent the archaic or generalised type of the family. In the Voles, or the more specialised Cricetines, the cusps of the molars have become modified into triangular prisms alternately arranged (fig. 1294), and

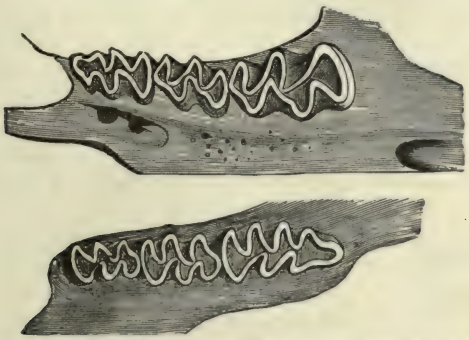


Fig. 1294.—The left upper and lower molars of the Water-Vole (*Arvicola amphibius*). Enlarged.

the roots are generally not developed, so that the crowns are hypsodont. *Siphneus*, which connects this family with the preceding, is found at the present day in Central Asia, and is represented by a living species in the Pleistocene of the Altai, and by another, which is extinct, in the Pliocene of Northern China. Of *Arvicola* (*Microtus*[1]), and *Lemmus* (including *Cuniculus*), there are numerous species in the Pleistocene of Europe, some of which are identical with living forms, while others are extinct; the former genus being also represented in the Forest-bed and the Coralline Crag. The allied *Fiber*, of North America, occurs also in the Pleistocene of the same country. In the typical or less specialised forms, the molars usually

[1] This name, as being earlier than *Arvicola*, is adopted by several recent writers.

have simple cusps, and are rooted. *Paciculus*, from the Miocene of the United States, is allied to the next genus, but has enamel-folds to the molars. *Neotoma* is represented by a species in the Pleistocene of the Pennsylvanian caves, which is perhaps not distinct from the living Florida-Rat. The genus *Cricetus*, typically represented by the European Hamsters, is taken by Mr O. Thomas to include the American *Hesperomys*. It is represented sparingly in the Pleistocene of Europe; but it is probable that *Cricetodon* (*Decticus*), which ranges from the Quercy Phosphorites to the Middle Miocene of France, cannot be generically separated. In America fossil forms occur abundantly in the Brazilian cave-deposits, where they have been described as *Hesperomys;* and it is probable that we must include in the same large genus (*Cricetus*) the so-called *Eumys* of the Miocene of North America. The subfamily *Deomyinæ* is only known by *Deomys*, of the Congo Valley, which has upper molars intermediate in structure between those of the preceding and following subfamilies. The *Murinæ*, or more specialised Mice, are mainly characteristic of the Old World, and do not date back far in time. Their upper molars have the cusps or tubercles arranged in three longitudinal rows and well-developed roots. *Mus*, or the closely allied *Acomys*, is first known from the Pliocene Pikermi beds, and thence is found through the Pleistocene of Europe. The Australian genera *Hapalotis* and *Mastacomys* are represented by existing species in the cave-deposits of that country. The Indian *Phlæomyinæ*, having broad upper incisors, and rooted molars with transverse laminæ, are represented in the Pleistocene of *Madras* by two species of *Nesocia* identical with those now inhabiting the same area. The *Gerbillinæ* also have laminated molars (fig. 1295), but the upper incisors are narrow and the hind limbs elongated. The existing *Gerbillus indicus* occurs fossil in the Madras caves. The last molar in both the upper and lower jaws of this genus has only a single transverse lamina, as shown in the figure. Lastly the *Sminthinæ*, in which there is a premolar in the upper jaw, are represented by the existing *Sminthus vagans* in the Pleistocene of Europe.

Fig. 1295.—The left ramus of the mandible, and the lower molars (enlarged) of *Gerbillus indicus;* from a cave in Madras.

Family Myoxidæ.—In the Dormice the number of the cheek-teeth is *Pm.* $\frac{1}{1}$, *M.* $\frac{3}{3}$; these being rooted, with complex enamel-folds. For palæontological purposes all the forms may be included in *Myoxus*, which commences in the Paris gypsum and Quercy Phosphorites, and is represented in the Pleistocene of Malta by a

species of the size of the Guinea-pig. The so-called *Brachymys* of the German Miocene appears to be generically the same.

As Myomorpha, of which the affinities are uncertain, may be mentioned *Heliscomys*, of the North American Miocene, in which there are four lower cheek-teeth, and the lower incisors are compressed and grooved; and *Eomys* (or *Omegodon*), from the Quercy Phosphorites, in which the cheek-teeth are *Pm.* $\frac{1}{1}$, *M.* $\frac{3}{3}$. *Colonomys*, from the North American Miocene, also belongs to this section.

Family Castoridæ.—With this family we enter the Sciuro-

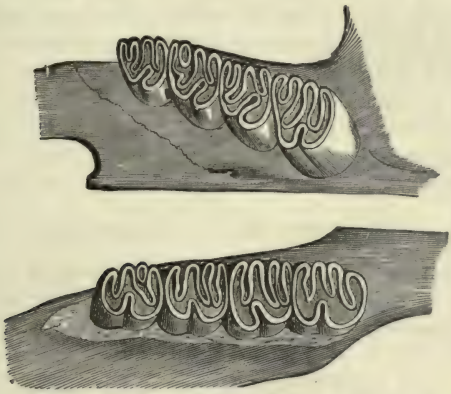


Fig. 1296.—Palatal aspect of the right upper and lower cheek-teeth of the Beaver (*Castor fiber*). The tooth on the right of each figure is the premolar.

morpha, which includes all the remaining Rodents. The Beavers are natatorial Rodents, with *Pm.* $\frac{1}{1}$, *M.* $\frac{3}{3}$; the cheek-teeth being semi-rooted or rootless, with re-entering enamel-folds (fig. 1296). *Castor* is represented by the existing Beaver in the European Pleistocene, and by an allied form in the Pliocene of the Auvergne; and also occurs in the Miocene of North America, where it has been named *Eucastor*. There has been great dispute as to the affinities of the great extinct Beaver (fig. 1297) of the Norfolk Forest-bed and Norwich Crag, but it is regarded by Mr Newton as identical with both *Trogontherium* of the Russian, and *Diobroticus* of the French Pleisto-

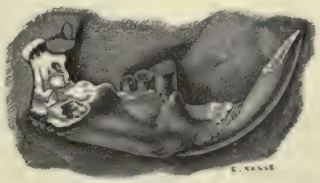


Fig. 1297.—Right ramus of the mandible of *Trogontherium Cuvieri*; from the Forest-bed. One-fourth natural size. (After Owen.)

cene. An allied genus is *Chalicomys* (*Steneofiber*), in which the humerus has a foramen, and the molars (fig. 1293, c) are more distinctly rooted, with shallower enamel-folds; it occurs in Europe in the Middle and Lower Miocene, and also in the Miocene of North America; *Palæocastor* from the latter deposits being apparently closely allied.

Family Ischyromyidæ.—*Ischyromys* (with which *Tillomys* is apparently identical) is a North American Miocene genus with *Pm.* $\frac{2}{1}$, *M.* $\frac{3}{3}$; having dental characters of the *Sciuridæ*, but otherwise resembling the *Hystricidæ* and *Caviidæ*, and thus indicating that the sections into which the existing Rodents are divided will not hold good for all the fossil forms. *Pseudotomus* from the White River Miocene is an allied form; while *Sciuromys* of the Quercy Phosphorites is probably also related. *Mysops* of the North American Eocene, according to Dr Schlosser, may be the same as *Ischyromys*. *Gymnoptychus* (p. 1421) may also be allied.

Family Sciuridæ.—In this family the cheek-teeth are usually *Pm.* $\frac{2}{1}$, *M.* $\frac{3}{3}$, but in *Sciurus* the first upper premolar is often absent. The molars are rooted, and, with the exception of *Eupetaurus* of Kashmir, are brachydont; those of the upper jaw usually having triangular or squared crowns, with two or more shallow infolds of

Fig. 1298.—Side view of the skull of *Cynomys Ludovicianus*.

enamel from the outer side (fig. 1299). The Marmots and their allies (fig. 1298) have uncompressed incisors; and the type genus *Arctomys* is represented by the existing *A. marmotta* (fig. 1299) in the Pleistocene of Europe, and by another species in that of North America. *Plesiarctomys* (with which *Sciuravus*, Marsh, and *Paramys*, Leidy, are identical) occurs in the Middle Tertiaries of both Europe and the United States, and connects *Arctomys* with *Sciurus*. *Spermophilus*, or the Sousliks, has both living and extinct

species in the Pleistocene of Europe; while the allied *Plesispermophilus* has been described from the Quercy Phosphorites. Among the Squirrels, of which the living genera have compressed incisors, *Sciurus* itself ranges down to the Quercy Phosphorites in Europe, and in North America occurs in the White River Miocene; the common existing *S. vulgaris* being found in the Norfolk Forest-bed. The recent northern genus *Tamias* occurs in the Pleistocene of Europe and Nebraska; while *Pseudosciurus* and *Sciuroides* are allied extinct genera from the Upper Eocene of the Continent, in both of which the molars are more elongated than in *Sciurus*. *Gymnoptychus*, with $Pm.\ \frac{1}{1}$, $M.\ \frac{3}{3}$, from the Miocene of North America, has more complex molars, and thereby approaches *Pteromys;* while *Meniscomys* (with which *Allomys* is apparently identical), with $Pm.\ \frac{2}{1}$, from the same deposits, presents some resemblances to the American *Haplodontidæ* (which, like the *Anomaluridæ*, are unknown in a fossil state), *Sciurodon* from the Quercy Phosphorites is regarded as a closely allied genus.

Fig. 1299. — Palatal view of the right upper and lower dentition of the Marmot (*Arctomys marmotta*). Recent and Pleistocene, Europe. The two teeth on the right side of the upper figure are the premolars.

Finally, we may here mention the small *Decticadapis*, of the Lower Eocene of Rheims, which appears to be a Rodent, although its affinities cannot yet be determined.

Order VIII. Carnivora.—Although the existing Carnivora can be defined with fair exactness, yet the fossil forms here included in this order render such definition almost or quite impossible. All the known forms are, however, unguiculate, with never less than four digits to each foot, all of which bear claws; and the pollex and hallux are never opposable. The dentition is diphyodont and heterodont, and (with the exception of the canines of the *Trichechidæ*) the teeth have closed pulp-cavities. The incisors are very generally three in number, the third being the largest; the canines are strong, pointed, recurved, and larger than the incisors; while the first pair of incisors never have an interval between them. The cheek-teeth vary, but are usually compressed in the anterior part of the series; while if the molars are tuberculate, they are not complex and divided into lobes by deep infolds of enamel. The condyle of the mandible forms a transversely elongated half-cylinder, working in a deep glenoid fossa, protected by a large postglenoid process. The

clavicle is never complete, and is frequently absent; the radius and ulna and the tibia and fibula are always distinct; but the scaphoid and lunar of the carpus very frequently coalesce. In a large number of cases the humerus has an entepicondylar foramen. The majority of the species subsist on animal food. In the more specialised types there is a tendency to a reduction in the number of the cheek-teeth, more especially the true molars.

As in the Rodents and the following orders, the manus is susceptible in most cases of the movements of pronation and supination; the head of the radius being accordingly freely movable in the lesser sigmoid cavity of the ulna. The proximal extremity of the latter bone is shown in the accompanying woodcut in order to exhibit the characteristic features obtaining in the unguiculate orders. Some observations on the phylogeny of the order will be found under the head of the Creodonta.

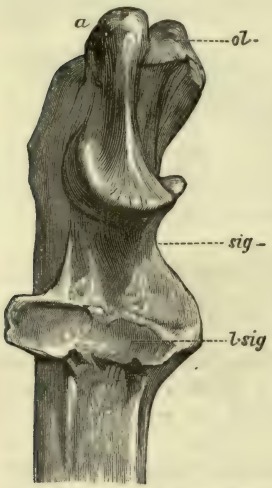


Fig. 1300.—Anterior aspect of the proximal extremity of the right ulna of *Hyænarctus;* from the Siwalik Hills. Reduced. *ol*, Olecranon; *a*, Anterior tubercle of do.; *sig*, Sigmoid cavity; *l.sig*, Lesser do. for head of radius.

The Carnivora are divisible into the suborders Pinnipedia, Carnivora Vera, and Creodonta; the latter being the most generalised.

Suborder 1. Pinnipedia.—This suborder comprises the typical Seals (*Phocidæ*), the Walruses (*Trichechidæ*), and the Eared, or Fur, Seals (*Otariidæ*); all of which mainly differ from the typical Carnivora in points connected with their subaquatic life. The brain is relatively large, with its hemispheres much convoluted, and broad in proportion to their length. The limbs are short, and are each furnished with five digits, which are connected by a web: in the hind feet the first and fifth digits are stouter, and generally longer, than either of the others. In the *Phocidæ* the hind feet when walking are directed backwards parallel to the axis of the body, but in the *Otariidæ*, which are the least aberrant members of the suborder, they are turned forwards. The dentition varies, but at least three kinds of teeth are always present. The canines are long and pointed; the cheek-teeth (fig. 1301), which usually comprise four premolars and one true molar, are not differentiated into carnassials and tuberculars, but are usually sharply pointed and often furnished with fore-and-aft basal cusps, although they are blunt and rounded in the Walrus. There is always a diminution of the incisors below

the typical number of $\frac{3}{3}$. The milk-teeth are very minute, and are either shed or absorbed at a very early date. The structure of the cranium approximates to that of the Bears and their allies. The larger limb-bones present very characteristic features, which enable them to be readily recognised in the fossil state. No fossil forms have been hitherto found which tend to throw any light upon the origin of this suborder; but in the reduction of the number of the incisors, they agree with some of the Creodonts, from which group they may be directly derived.

Family Phocidæ.—The number of incisors in this family varies from $\frac{2}{1}$ in *Cystophora* to $\frac{3}{2}$ in *Phoca* and *Halichœrus*. The best known fossil Seals have been obtained from the Pliocene Crag of Antwerp, and have been referred to the following genera, of which

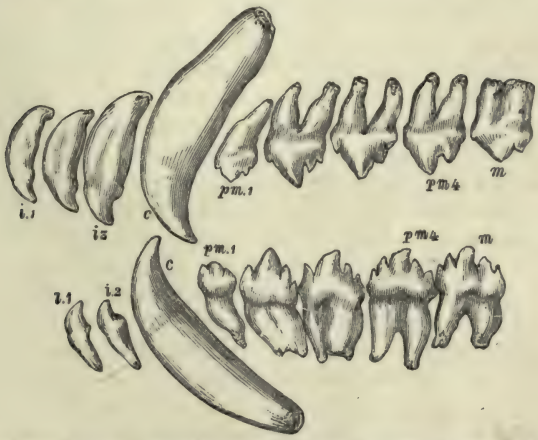


Fig. 1301.—Lateral view of the left dentition of *Phoca*. Reduced. Letters as in fig. 1302.

all but the first are peculiar to the Tertiary, although it may be a question whether all of them are rightly distinguished from existing genera. They comprise *Phoca*, represented by a species allied to the Common Seal (*P. vitulinoides*); *Callophoca* allied to the Greenland Seal (*P. grœnlandica*); *Platyphoca* to the Bearded Seal (*P. barbata*); *Phocanella* to the Ringed Seal (*P. fœtida*); *Gryphoca* to the Grey Seal (*Halichœrus*); *Palæophoca* and *Monatherium* to the Monk Seal (*Monachus*) of the Mediterranean; *Mesotaria* to the Bladder Seal (*Cystophora*); and *Prophoca* which does not appear closely allied to any existing form. Remains of *Phocidæ* in other formations are rare; but a species provisionally referred to the type

genus has been obtained from the Miocene of Malta, while other forms occur in the Pliocene of the Crimea and elsewhere. Remains from the Miocene of Virginia have been described under the name of *Phoca Wymani*, and others from the Pliocene of South Carolina have likewise been referred to the same genus.

Family Trichechidæ.—The Walruses, which are in some respects intermediate between the other two families, are readily distinguished by their enormous upper canines. The existing Arctic *Trichechus rosmarus* occurs fossil in the Norfolk Forest-bed, and an allied species, *T. Huxleyi*, in the Red Crag; while the names *Alachtherium* and *Trichechodon* have been applied to closely allied, if not generically identical, forms from the Belgian Crag.

Family Otariidæ.—This family, in which the number of the incisors is invariably $\frac{3}{2}$, is almost unknown in a fossil state, although some writers have considered that certain genera here included in the *Phocidæ* should be referred to it. Remains of existing species of the type genus *Otaria* have, however, been obtained from Prehistoric or Pleistocene beds in New Zealand, and also from the Pleistocene of South America.

Suborder 2. Carnivora Vera.—In the typical Carnivora the brain is relatively large, and the hemispheres are elongated, and always marked by three or four folds. The fore limbs never have the first digit, or the hind limbs the first and the fifth digits longer than all the rest. There is always a more or less distinctly defined *carnassial* tooth in each jaw; the teeth in front of such carnassial being always more or less compressed and pointed, while those behind the same are broad and tuberculated. And it appears from the dentition of the suborder Creodonta that these tuberculated posterior teeth are the most specialised. The upper carnassial (p^4, fig. 1302), as being the hindmost of those teeth which have milk predecessors, is reckoned as the last premolar; and it usually consists of an outer compressed blade, generally furnished with two (fig. 1302), but occasionally (fig. 1325) with three cusps or lobes, and of an inner tubercle (fig. 1325). This tubercle is generally placed near the anterior extremity of the crown, and is of medium size; but in some instances, as in *Machærodus* (fig. 1334), it may be almost absent, while in others, as in the Otters (fig. 1303), it attains a great development. The lower carnassial (m^1 in the mandible of fig. 1302), as the most anterior of the teeth without milk predecessors, is reckoned as the first of the true molar series. Typically, the crown of this tooth (fig. 1302) consists of an anterior blade, composed of two compressed cusps or lobes, and an inner cusp (fig. 1318), and of a hind talon. In the Wolf (fig. 1302) all these elements are well developed; but sometimes, as in *Felis*

(fig. 1331), both the inner cusp of the blade and the talon may be entirely wanting; or, again, the talon, as in *Ursus* (fig. 1309), may attain excessive development, and the blade be proportionately reduced; the cusps or lobes of the latter being in such cases placed obliquely.

Although the foregoing terms are those generally used in describing the carnassial teeth, a few words may be said as to the serial homology of their cusps. Thus, in the normal type of upper carnassial with two

Fig. 1302.—Outer lateral view of the left dentition of the Wolf (*Canis lupus*). Reduced. *i*, Incisors; *c*, Canine; *p*, Premolars; *m*, True molars.

lobes to the blade (fig. 1318, *pm.* 4), it appears that the inner tubercle represents the protocone of the tritubercular type (p. 1275), the first lobe of the blade corresponding to the paracone, and the second to the metacone. In those forms with a trilobed blade (fig. 1325), the anterior lobe is a superadded element not found in the primitive type. In the lower carnassial (compare fig. 1145, p. 1275) the posterior lobe of the blade, which is really external, is the protoconid; the anterior lobe (paraconid) and the inner cusp (metaconid) are both internal; while the talon is the hypoconid.

With very few exceptions, the incisors are $\frac{3}{3}$ in number. The digits are nearly always furnished with long, sharp, and more or less curved claws, which in the true Cats (*Felis*) can be retracted into protecting bony sheaths. In some genera, like *Ursus*, the whole of the sole of the foot is applied to the ground in walking (*plantigrade*), while in others, like *Canis*, only the terminal digits are so used (*digitigrade*). As a feature of some importance in this suborder,

mention must be made of the *alisphenoid canal*, which is a short bony channel situated in the alisphenoid bone immediately on the outer side of the pterygoid. The existing representatives of this suborder have been divided into three sections—the Arctoidea, Cynoidea, and Æluroidea; but extinct forms show such a complete transition between the three that it is impossible to adopt any divisions of higher rank than families, and scarcely any two writers agree as to the limits of the latter. It is, moreover, very doubtful whether the Arctoidea is really a natural group. When, indeed, we go back to the Upper Eocene or Lower Oligocene, where this suborder is first definitely known, we find that Bears pass imperceptibly into Dogs, Dogs into Civets, Civets into Hyænas and Cats, while Weasels appear to be related to the Civets; and the principles adopted in the classification of recent forms consequently fail to enable us to make any really satisfactory arrangement.

Family Mustelidæ.—This family comprises the Sea-Otters, Otters, Badgers, and Weasels. In all existing forms the skull has no alisphenoid canal; there is never more than one upper true molar, and the lower true molars are nearly always two, although reduced to one in *Mellivora*. The upper true molar has its inner tubercular portion wider than the outer or cutting moiety (fig. 1306), this feature being most developed in the Otters (fig. 1303); and the

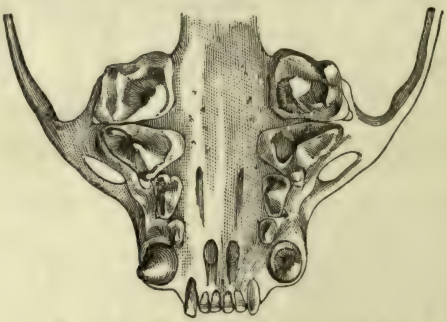


Fig. 1303.—Palate of *Lutra cinerea*; India.

cusps of the blade of the lower carnassial are comparatively low (fig. 1308). The palate is comparatively wide, and the premolars are somewhat crowded together; while the auditory bulla has no septum, and is usually, but slightly, inflated. It is suggested by Dr Scott that the *Mustelidæ* are a branch from the primitive *Viverridæ*, and there is considerable evidence in favour of this view, which, if true, at once breaks up the Arctoidea.

The existing *Lutrine* section may be palæontologically divided into *Lutra* and *Enhydra*; the latter being a marine form unknown

in a fossil state. The species of *Lutra* are characterised by the great constriction of the skull in the orbital region, and usually by the more or less squared contour of the crown of the upper true molar, and the great development of the inner tubercle of the last upper premolar, which forms a crescentoid ridge; both these features being well shown in fig. 1303. In the typical *L. vulgaris* the dental formula is *I.* $\frac{3}{3}$, *C.* $\frac{1}{1}$, *Pm.* $\frac{4}{3}$, *M.* $\frac{1}{2}$, but in some existing species the first upper premolar may be absent (fig. 1303), and other variations occur in fossil forms. This genus may be divided into three groups, which it is quite permissible to regard as distinct genera, and of which the first and third are extinct. The *Enhydriodont*, or most specialised group, comprises two large otters respectively from the Pliocene Siwaliks of India and the Middle Miocene of Italy, which attained dimensions fully equal to those of the existing *L. brasiliensis*. In both these forms the first upper premolar is absent, and in the Indian *L. sivalensis* the second premolar may likewise disappear. In this species, moreover, the fourth upper premolar or carnassial (fig. 1305) differs from that of all other otters in that the inner crescent consists of three distinct tubercles; but the Italian *L. Campanii* (fig. 1304) connects in this respect the Indian species with the true otters. The typical group, which includes all the existing forms, is known to date from the Middle Miocene of Europe, and also occurs in the Tertiaries of America and the Indian Siwaliks. Remains of the existing *L. vulgaris* occur in the Norfolk Forest-bed; while the Siwalik *L. palæindica* is closely allied in the structure of its teeth and skull to the living hairy-nosed otter (*L. sumatrana*) of Asia. Finally, the *Lutrictine* group is represented only by *L. Valetoni*, of the Lower Miocene of the Continent, which is distinguished from all other Mustelines by the presence of a minute second upper true molar. This species is also characterised by the narrowness of the first upper true molar, and by the circumstance that the anterior upper premolars are placed immediately behind the canine, instead of being squeezed towards its inner side, as in fig. 1303. If regarded as generically distinct, this form should be known as *Potamotherium*. The Miocene *Trochictis* appears to connect the Otters with the Weasels.

Fig 1304.—The right upper carnassial of *Lutra Campanii*; from the Miocene of Italy. In its natural position the outer ridge would be oblique, as in fig. 1303.

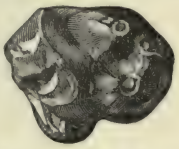


Fig. 1305.—The left upper carnassial of *Lutra sivalensis*; from the Pliocene of India. The outer ridge is broken.

Among the Badgers and their allies extinct species of the type

genus *Meles* occur in the Pliocene of Persia, the common Badger (*M. taxus*) being found in the Pleistocene of Europe; while extinct species of *Mellivora*, or Ratel (fig. 1306), have been described from the Pliocene of India, this genus being confined to that country

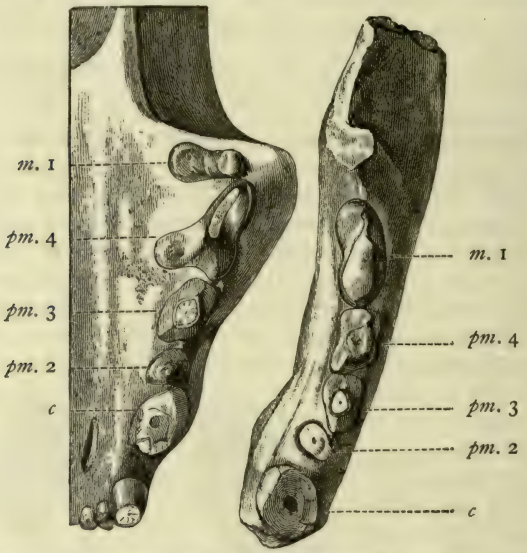


Fig. 1306.—The right upper and left lower dentition of *Mellivora sivalensis*; from the Pliocene of India.

and Africa. The last-named deposits also yield the extinct *Mellivorodon*. Species of the American genus *Mephitis* (*Conepatus*) occur in the Pleistocene cave-deposits of Brazil; while *Promephitis*, of the Pliocene of Greece, is considered to be allied. *Palæomephitis*, of the Miocene of Bavaria, which has been placed in this family, appears to be identical with *Viverra*.

The Weasels, or typical representatives of the family, which are divided into the existing genera *Mustela* (including *Putorius*), *Gulo*, and *Galictis*, occur commonly throughout the higher Tertiaries. *Mustela* (fig. 1307), in which the premolars vary from $\frac{3}{3}$ to $\frac{4}{4}$, and the inner cusp of the lower carnassial is frequently absent, is represented by numerous existing species in the Pleistocene of Europe, and by a number of extinct forms, some of which it has been proposed to separate under the names of *Plesiogale* and *Palæogale*, ranging down to the Quercy Phosphorites. A large species (fig. 1308) occurs in the Siwaliks of India, which was probably closely allied to *M. flavigula* of the same regions; and other large forms are

found in the Miocene of Bavaria, and the Pliocene of Greece and Persia; while the genus is also represented by a smaller species in the Pliocene of North America. *M. Larteti* of the Miocene of Sansan should perhaps be referred to the African genus *Ictonyx*.

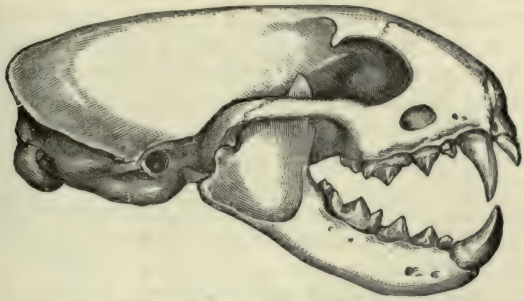


Fig. 1307.—Right lateral view of the skull of the Polecat (*Mustela putorius*).

The extinct *Plesictis* occurs in the Lower Miocene and Upper Eocene (Oligocene) of Europe, and is characterised by the presence of $\frac{4}{4}$ premolars, and the circumstance that the temporal ridges of the cranium do not unite to form a sagittal crest, as they do in *Mustela*. The inner portion of the upper true molar, as in some of the Miocene species of *Mustela* (*Palæogale*), becomes narrower than the outer, and the auditory bulla is more inflated; both these features indicating affinity with the Viverrine genus *Stenoplesictis*. The existing genus *Galictis* of America is represented in the Pleistocene of the two divisions of that Continent; while the Arctic *Gulo* occurs in the Pleistocene of Europe, where remains of the existing Wolverine (*G. luscus*) are met with.

Fig. 1308.—Upper and outer view of the left lower carnassial of *Mustela*; from the Pliocene of India.

Family Procyonidæ.—The *Procyonidæ* may be taken to include both the American Racoons and Coatis and the Indian *Ælurus*, but are of small palæontological importance. In all living genera the true molars are $\frac{2}{2}$ in number; and the American forms have no alisphenoid canal. *Nasua* (Coati) occurs fossil in the Pleistocene of Brazil; and the extinct *Cynonasua*, characterised by the presence of three lower true molars, is found in the older *infra*-Pampean of Patagonia. *Procyon* (Racoon) is represented in the Pleistocene of North America; while *Leptarctus* from the same deposits, and *Arctodus* from the Pleistocene of South Carolina, are extinct genera

connecting the present family with the next. *Ælurus* is represented at the present day by a single species from Nipal and the adjacent regions. In common with the American members of the family it is characterised by the second lower true molar being longer than the first, and by the absence of a "carnassial" character in the latter. The molars are, however, of an unusually complex character; and the last one of the lower jaw presents a decided approximation to the third molar of certain Ungulates. The only fossil that has been referred to this genus is a fragment of a mandible with the last true molar from the Red Crag of Suffolk. It is, however, advisable to await further information before admitting this determination as certain.

Family Ursidæ.—Palæontologically it appears advisable to include in this family not only the Bears, but also the Dogs (*Canidæ*), since the passage from one type to the other is so complete as to render it impossible to draw any satisfactory distinction between them. Although no precise definition of this family can be given, the following points may be noticed. With the exception of the

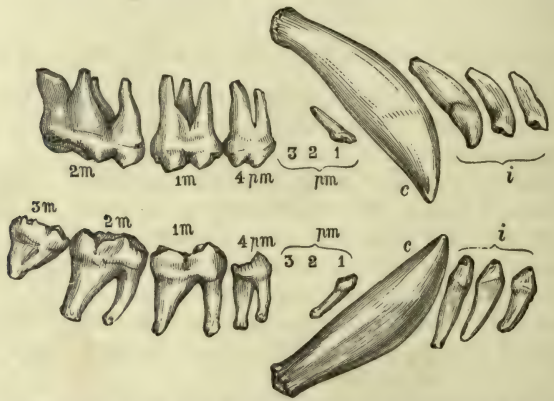


Fig. 1309.—Outer view of the right dentition of the Polar Bear (*Ursus maritimus*). Reduced. *i*, Incisors; *c*, Canine; *pm*, Premolars; *m*, True molars.

existing genus *Ælurops* the skull has an alisphenoid canal. The upper true molars are frequently two in number, but they may be reduced to one (*Icticyon*), or increased to three (*Amphicyon*) or four (*Otocyon*); while the corresponding teeth of the lower jaw are nearly always three in number, although they may be reduced to two, and in *Otocyon* are augmented to four. The first upper true molar is invariably placed behind the carnassial, and the latter generally has two lobes. The upper true molars may have either oblong (*Ursus*), squared (*Hyænarctus*), or triangular crowns; and the talon of the

lower carnassial is well developed. The auditory region may either have a depressed bulla, without an inner septum (*Ursus*), as in the existing *Mustelidæ*, or (*Canis*) may have an inflated bulla with an incomplete septum approximating to that of the *Viverridæ*. The least

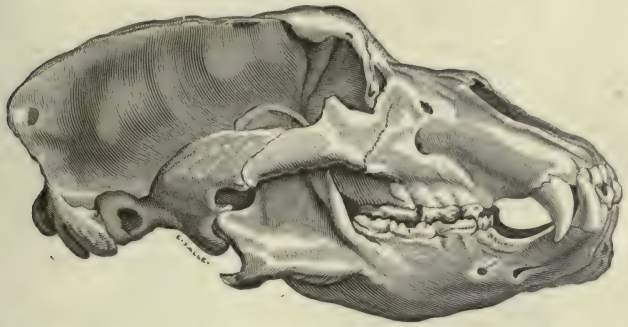


Fig. 1310.—Right lateral aspect of the skull of the Cave-Bear (*Ursus spelæus*); from the Pleistocene of Germany. Reduced.

specialised forms have an entepicondylar foramen to the humerus, and a third trochanter to the femur. The feet are digitigrade in *Canis* and plantigrade in *Ursus*. In common with the majority of the Carnivora Vera, and also many of the Creodonta, the second lower incisor is thrust up above the line of the first and third.

In the type genus *Ursus* the dental formula is usually *I.* $\frac{3}{3}$, *C.* $\frac{1}{1}$, *Pm.* $\frac{4}{4}$, *M.* $\frac{2}{3}$, but in *U.* (*Melursus*) *labiatus* the number of the incisors is reduced to $\frac{2}{3}$. The second and third premolars are usually shed at an early age; the upper carnassial (*pm.* 4, fig. 1309) is shorter than the first true molar, and lacks the marked sectorial character which it presents in most other Carnivora; and the upper true molars are greatly elongated, and have flat tuberculated crowns. The foramen has disappeared from the humerus; and the olecranon of the ulna (fig. 1311) has become very short; while the femur has no third trochanter. This genus may be regarded as in some respects very specialised, although retaining generalised features in its plantigrade and pentedactylate feet. It is of com-

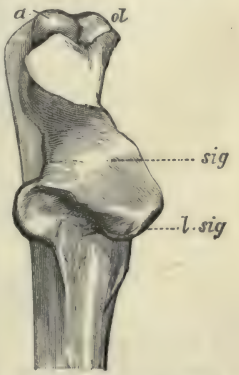


Fig. 1311.—Anterior aspect of the proximal extremity of the right ulna of *Ursus arctus*. One-half natural size. Letters as in fig. 1300.

paratively modern origin; the earliest known species being *U. Theobaldi*, of the Pliocene of India, which was the ancestor of the existing *U. labiatus* of the same country. The last-named species is found in a fossil state in the caves of Madras. In the Upper Pliocene of Europe we have the small *U. etruscus;* and in the Pleistocene of the same area the existing European Brown Bear (*U. arctus*), the allied or identical North American Grizzly (*U. horribilis*), and the huge extinct *U. spelæus*, or Cave-Bear (fig. 1310). The latter species is characterised by the prominent ridge above the orbits, and the extremely fine tuberculation of its molars; its remains are found in extraordinary abundance in the bone-caves

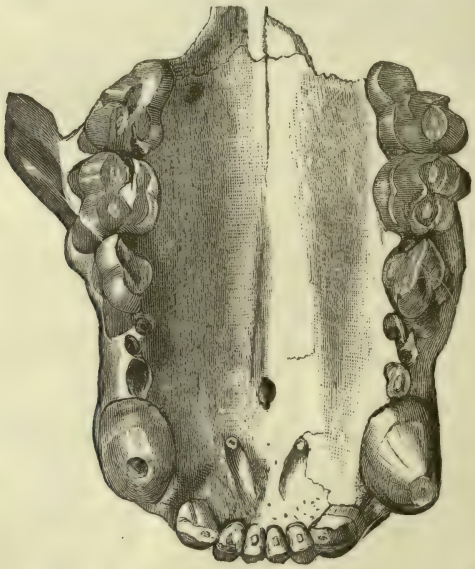
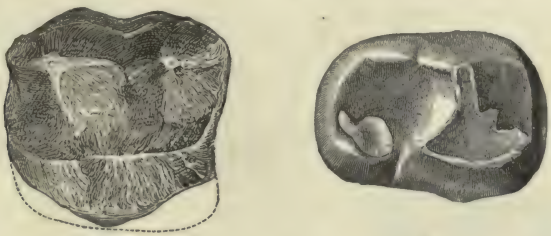


Fig. 1312.—Palate of *Arctotherium bonariense;* from the Pleistocene of South America. One-fourth natural size.

of the Continent. Very noteworthy is the occurrence of abundant remains of Bears in the caverns of North Africa, since but one living species is found in the whole of that vast continent. In the Pleistocene of South America and California we meet with the huge *Arctotherium* (fig. 1312), in which the upper carnassial is relatively longer than in *Ursus*, while the crowns of the true molars are more nearly square; so that its dentition serves to connect that of *Ursus* with that of the next genus. According to Professor Cope the humerus has a foramen. The genus *Hyænarctus* occurs first in the Middle Miocene of Europe, where the species are of small size

(fig. 1313), and is represented by much larger forms in the Pliocene of India, China, and Europe. In this genus the proximal extremity of the ulna (fig. 1300) has an elongated olecranon similar to that of *Amphicyon* and *Canis*. There is also a third lobe to the upper carnassial (whereby it resembles the corresponding tooth of *Hyæna*), while the first upper true molar is square (fig. 1314) in one species, and imperfectly triangular in another; the lower carnassial resembling that of *Canis*. The small *H. anthracitis* of the Middle Miocene of Italy may be identical with *H. minutus*. Before noticing the forms connecting *Hyænarctus* with *Canis*, we must mention some extinct genera more or less nearly allied to the present group, and which Dr Schlosser also regards as related to the *Procyonidæ*. Among these are *Simocyon* (*Pseudocyon* or *Metarctus*) of the Pliocene of Greece and Hungary, in which the number of the cheek-teeth is *Pm.* $\frac{2}{(2-4)}$, *M.* $\frac{2}{2}$; and *Enhydrocyon* (fig. 1315), of the Miocene of North America, in which the cheek-teeth number *Pm.* $\frac{3}{3}$, *M.* $\frac{2}{2}$, the cranium is very short, and the lower carnassial has a cutting talon. *Oligobunis* of the Miocene, and *Tomarctus* of the Pliocene of the same country are also more or

Fig. 1313.—Outer and palatal aspects of the left upper true molars of *Hyænarctus minutus*; from the Middle Miocene of Silesia. (After Koken.)



A B

Fig. 1314.—First upper (A) and second lower right true molar (B) of *Hyænarctus*; from the Pliocene.

less nearly related types. Here we may also place *Hyænocyon* of the Miocene and *Ælurodon* (*Prohyæna*) of the Pliocene of North America, though Dr Schlosser, on wholly insufficient grounds, would refer both to the *Hyænidæ*. The former has the molars

reduced to $\frac{1}{1}$; while in the latter the upper carnassial has three lobes like *Hyænarctus*, the number of teeth according to Professor Cope being the same as in *Canis*, and the humerus having no foramen. More nearly allied to the *Hyænarctus* group is *Cephalogale*,

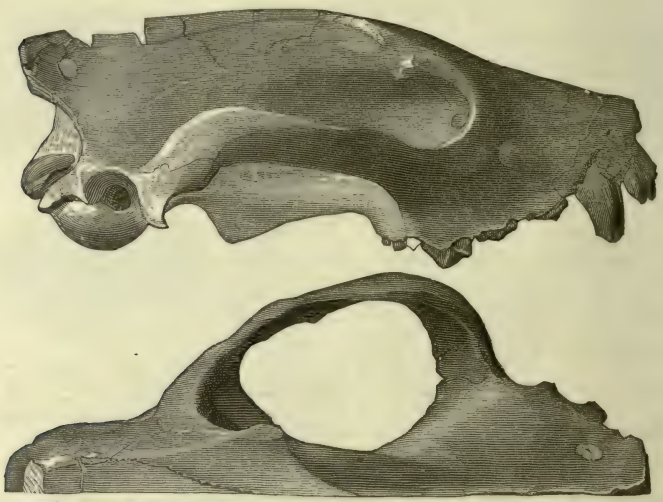


Fig. 1315.—Lateral and upper view of one-half of the cranium of *Enhydrocyon stenocephalus*; from the Miocene of North America. One-half natural size. (After Cope.)

in which the two upper true molars (fig. 1316) become more or less triangular, but the carnassial in both jaws (figs. 1316, 1317) is comparatively short, with low cusps. This genus, according to Dr Schlosser's emendation, is comparatively abundant in the Upper Eocene and Lower Miocene of the Continent; many of the species having been included by Dr Filhol in *Cynodictis*. Extremely near to those species of *Hyænarctus* in which the upper true molars are triangular is the gigantic *Dinocyon* from the Middle Miocene of Europe, in which the above-mentioned teeth become perfectly triangular like those of *Canis*; and we may here mention *Brachycyon* from the Upper Eocene of France. The widely-spread genus *Amphicyon* (in which *Pseudamphicyon* of Dr Schlosser may be in part included) occurs in Europe from the Upper Eocene to the

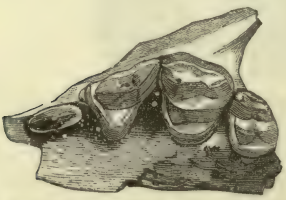


Fig. 1316.—The last four left upper teeth of *Cephalogale Gryei*; from the Upper Eocene of France.

Middle Miocene of Europe, and is also found in the Pliocene of India; the forms from the Upper Eocene of North America which have been referred to it, are regarded by Dr Scott as distinct, and have been named *Daphænus*. Its teeth closely resemble those of *Canis*, but there are three upper true molars; the femur has, however, a third trochanter, the feet are plantigrade and pentedactylate, the distal end of the humerus has a foramen, and the auditory bulla is somewhat inflated, with either a very rudimentary or no septum.[1] This genus has therefore the dentition of a Dog, coupled with limbs more like those of a Bear; and it is a curious comment on the attempt to maintain the families *Canidæ* and *Ursidæ* that while Professor Flower places *Amphicyon* in the former, Dr Schlosser refers it to the latter. This genus is evidently a very

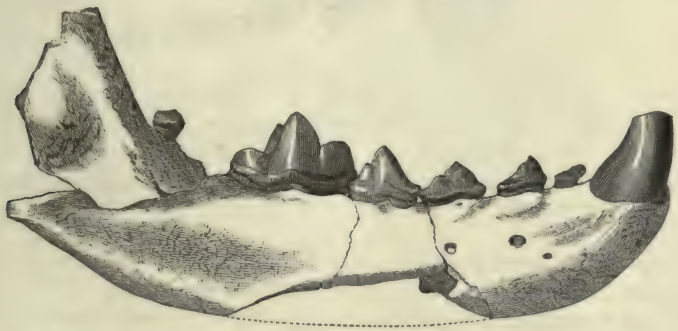


Fig. 1317.—Right ramus of the mandible of *Cephalogale brevirostris*; from the Upper Eocene of France.

generalised form, from which many others may have been derived. In *Canis*, comprising the Dogs, Wolves, and Foxes, the dental formula is normally $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{4}{4}$, $M.\frac{2}{3}$, but in some forms (*Cyon*) the lower true molars may be reduced to two, and in others (*Lycorus*) there are but three lower premolars, while occasionally the third upper true molar is retained. The characteristic features of the teeth are shown in figs. 1302 and 1318; but it may be observed that the relative length of the carnassial and the degree of obliquity of the cusp-line in the lower carnassial varies in different species; the most specialised forms showing the greatest development of these features. The third lower premolar has a hinder basal cusp which is usually wanting in *Amphicyon;* the humerus has no foramen; the femur has lost the third trochanter; the feet are digiti-

[1] The general characters of the base of the skull of *Amphicyon* are Canoid, but in the presence of postparietal and mastoid foramina it agrees with the Bears.

grade; and the hallux is wanting in the pes. This genus probably commenced in the Upper Miocene of Œningen, and is widely distributed over all the world from the Pliocene upwards. The Wolf (*C. lupus*) ranges down to the European Pleistocene, and the allied *C. Cautleyi* is found in the Pliocene of the Siwalik Hills. *C. curvi-*

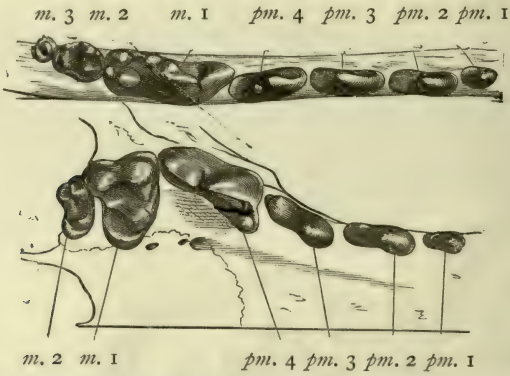


Fig. 1318.—Palatal aspect of right lower and upper dentition of *Canis argentatus*. The oblique line in the lower carnassial is the cusp-line. (After Huxley.)

palatus of the latter deposits shows signs of affinity with the African *Otocyon* (Fennec). *Lycaon*, now confined to Africa, and distinguished by having an anterior cusp to the last lower premolar, is found in the Pleistocene of Glamorganshire. *Palæocyon*, of the Brazilian Pleistocene, is regarded by Dr Schlosser as indistinguishable from *Canis*. *Temnocyon*, of the North American Miocene, has the talon of the lower carnassial secant, and a foramen to the hume-

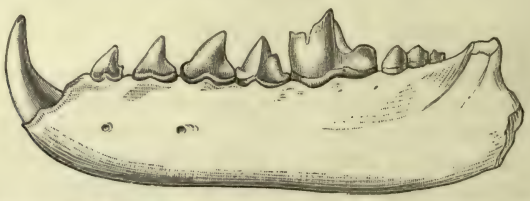


Fig. 1319.—Left ramus of the mandible of *Cynodictis lacustris*; from the Upper Eocene of France. (After Gaudry.)

rus; while in the existing American *Icticyon* (*Speothos*), which is represented in the Brazilian Pleistocene, the lower carnassial has not only a secant talon but also lacks the inner cusp. Perhaps, however, the most interesting genus of the whole group is *Cynodictis* (in which we may include *Cynodon*, *Amphicynodon*, and *Pachycyno-*

don), of the Upper Eocene and Lower Miocene of the Continent, and also of the White-river Miocene of North America, where it has been described as *Galecynus*. In this genus the dental formula is usually the same as in *Canis*, but in some cases (as in that genus) there are only two lower true molars. The teeth (figs. 1319, 1320) resemble also those of the *Viverridæ*, the carnassials being never very long, and the cusp-line of the lower one transverse; and the humerus has a foramen. The auditory bulla is inflated, but according to Dr Filhol, has no septum. This genus is, indeed,

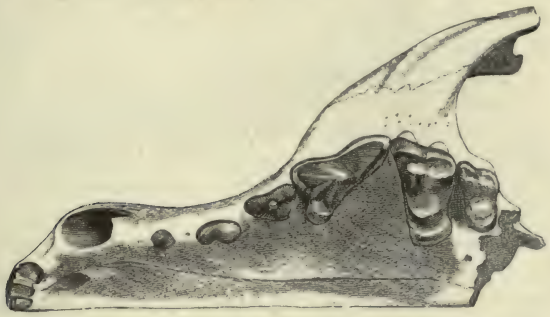


Fig. 1320.—Left half of the palate of *Cynodictis longirostris*; from the Upper Eocene of France.

one closely connecting the Canoids and Viverroids; and since it is pretty evident that the *Hyænidæ* and *Felidæ* are divergent branches from an early Viverroid stock it is probable that *Cynodictis* represents a type not far removed from the one which has given rise to several of the more specialised Carnivores, and is itself derived from *Amphicyon*, or an allied type.

Family Miacidæ.—This family is provisionally adopted to include the Eocene genera *Miacis* and *Didymictis*, which appear to be primitive forms allied to both Canoids and Viverroids, but which Professor Cope placed among the Creodonta. *Miacis* (= *Uintacyon* and *Viverravus*) occurs in the Upper, or Bridger, Eocene of North America, and according to Dr Schlosser, who places it with the Canoids, in both the Lower and Upper Eocene of France. *Didymictis* (*Limnocyon*), which occurs in the Puerco, Wasatch, and Bridger Eocenes of North America, is included by Dr Schlosser in the *Viverridæ*. *Dromocyon* is noticed on page 1453.

Family Viverridæ.—The Viverroids are comparatively small Carnivores, showing such close affinities in one direction with *Cynodictis* among the *Ursidæ*, in another with the *Mustelidæ*, and in a third with the *Hyænidæ* and the *Felidæ*, that their accurate definition is quite impossible. The skull in existing forms generally

has an alisphenoid canal; and the auditory bulla is inflated and has a complete septum. There are usually two true molars in each jaw, although the second is wanting in *Prionodon*. Those of the upper jaw (fig. 1322) are usually triangular, and are always narrower internally than externally, although they may be narrow in *Viverra* (fig. 1322) and very broad in *Paradoxurus;* and, except in *Cryptoprocta* are placed behind the carnassial. The cusps of the lower carnassial are generally very tall; the premolars are spaced; and the palate, like the entire skull, is long and narrow. The upper carnassial is subject to great variation in relative length. In typical forms the blade of the lower carnassial has an inner cusp, while its cusp-line is transverse, and the talon is relatively large. The humerus usually has an entepicondylar foramen. The feet are plantigrade, and usually have five complete digits; and their claws, as a rule, are comparatively straight and only slightly retractile, and are not protected by a bony sheath. Exclusive of *Miacis* and its allies, which are here regarded as representing a separate family, the *Viverridæ* are characteristic of the Old World. The Oriental genus *Paradoxurus*, characterised by its broad upper molars, is at present unknown in a fossil condition. The more widely spread *Herpestes* (Mongoose) is characterised by its narrow upper molars, by the presence of an inner tubercle to the third upper premolar, and of a hinder cusp to the fourth lower premolar. This genus is represented in a fossil state by remains of the existing *H. nipalensis* (fig. 1321) in the Pleistocene of India, and by extinct species in the Upper Eocene and Miocene of Europe. *Amphictis*, from the Lower Miocene (Upper Oligocene) of France, seems to be closely allied to *Viverra*, but the second lower true molar is longer and has two distinct roots. The type genus *Viverra* (fig. 1322), which has no inner tubercle to the third upper premolar, commences in the Upper Eocene of England and France (*V. Hastingsiæ* and *V. angustidens*), and occurs right through the succeeding Tertiaries till the Lower Pliocene of France, where it is represented by *V. Pepraxti*. The latter Civet, together with other allied species from the Pleistocene and Pliocene of India, presents, however, certain dental features in which it approximates to *Ictitherium*. The Oriental genus *Prionodon*, in which there is only one upper true molar, and the inner cusp of the lower carnassial is very small, while the humerus has a foramen, is not known to occur in a fossil state. So far as can be determined from the lower

Fig. 1321.—The right ramus of the mandible of *Herpestes nipalensis;* from the Pleistocene of Madras. All the teeth except the carnassial and the canine are wanting.

jaw, *Palæoprionodon*, of the Quercy Phosphorites, appears to be so closely allied to *Prionodon*, that it is somewhat difficult to see how it can be even generically separated. Closely allied to *Palæoprionodon* is *Stenoplesictis*, from the same deposits, in which the dental formula is *I.* $\frac{3}{3}$, *C.* $\frac{1}{1}$, *Pm.* $\frac{4}{4}$, *M.* $\frac{2}{2}$, or the same as in *Viverra*. This genus presents, however, decided indications of affinity with

Fig. 1322.—Palatal aspect of the left upper dentition of the Zibeth (*Viverra zibetha*); from India.

the Musteloid *Plesictis*, on which account it is placed by Dr Schlosser, together with *Palæoprionodon*, in the same family; but its dentition and the contour of the skull are decidedly Viverrine, and, according to Dr Scott, the bulla has a complete septum, of which the position is visible externally, as in modern Viverrines. It is, however, quite probable that we may have in these generalised

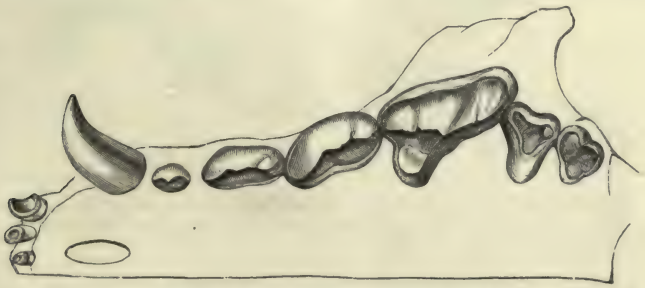


Fig. 1323.—Palatal aspect of the left upper dentition of *Ictitherium robustum*; from the Pliocene of Greece. (After Gaudry.)

forms the ancestral types of the *Mustelidæ*, which from this view will have lost the septum of the bulla independently of the Bears. In all the above-mentioned genera the upper carnassial has only two lobes, but in *Ictitherium* (*Thalassictis*) they are increased to three, as in *Hyæna*. *Ictitherium* occurs in the Lower Pliocene of Greece, Hungary, and France; and its upper true molars (fig. 1323) have

become relatively smaller than in *Viverra*, and in the figured species have a tendency to become placed on the inner side of the carnassial. The genus *Cryptoprocta*, which is unknown in a fossil state, approximates in the character of its dentition and its semi-retractile claws to the *Felidæ*.

Family Hyænidæ.—The above-mentioned genus *Ictitherium* may without much doubt be regarded as the ancestral type of the *Hyænidæ*, which form a family of comparatively recent origin and entirely confined to the Old World.[1] The transition to *Ictitherium* is indeed

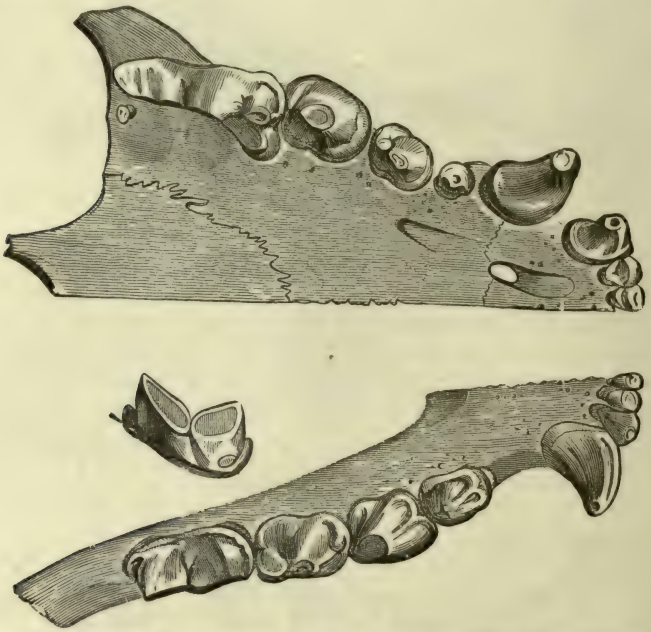


Fig. 1324.—Oral view of the right half of the palate and right ramus of the mandible of the Spotted Hyæna (*H. crocuta*), together with outer view of the lower carnassial tooth. One-half natural size.

so close that it is impossible to give a distinctive diagnosis of the family. Usually, however, there is but a single upper true molar, which is of small proportionate size, and is generally placed more or less entirely on the inner side of the carnassial; the latter tooth (fig. 1325) always having three distinct lobes to the blade, and a well-developed inner tubercle. The lower carnassial, or first true molar (fig. 1324) has a very large blade, and the hind talon com-

[1] This is exclusive of *Ælurodon* (*Prohyæna*) and *Hyænocyon*, which Dr Schlosser transfers from the *Ursidæ* to this family.

paratively small; while its inner cusp, if present, is likewise relatively small. There is never more than one lower molar ($\overline{m.\ 2}$) behind the carnassial, and if present that tooth is very small. In the existing genus the humerus has no entepicondylar foramen, while, at least in the living species, each foot has but four digits, of which the claws are non-retractile. The most generalised member of the family is the genus *Palhyæna*, of the Lower Pliocene of Greece, France, and Persia, which has been included by many writers in *Ictitherium*, but of which the carnassial teeth are essentially those of a Hyæna. The dental formula is $I.\ \frac{3}{3}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{4}{4}$, $M.\ \frac{2}{2}$, or the same as in *Viverra*. The first upper true molar is placed entirely on the inner side of the large carnassial; the lower carnassial, except for its rather larger talon, is almost indistinguishable from that of the Striped Hyæna, while the second lower true molar is comparatively small. The first lower premolar is very minute, and in their compressed crowns the other premolars are more like those of *Viverra* than those of existing Hyænas. The type species is comparatively small, with slender jaws, and the muzzle is elongated after the Viverroid fashion. The imperfectly known *Lepthyæna*, of the Indian Siwaliks, is closely allied to, if not identical with, the preceding genus. The remaining forms may be included in the genus *Hyæna*, which may be divided into groups corresponding to the genera of some writers, although there is an almost complete transition from one to the other. In all cases there is never more than a single upper true molar, while in existing forms the normal dental formula is $I.\ \frac{3}{3}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{4}{3}$, $M.\ \frac{1}{1}$. In some fossil forms, however, the first upper premolar may be absent, while in others there may be a small first lower premolar or a second lower true molar.

Of the more generalised forms classed in the *Lychyænine* group (*Lychyæna*), as represented by *H. macrostoma* of the Pliocene of India, and *H. chæretis* of that of Greece and Samos, the muzzle is long, the premolars, of which there are four in the lower jaw, are compressed, the first upper true molar is placed partially behind the carnassial, the lower carnassial has an inner cusp, and there was probably a second lower true molar. In the *Hyænictine* group (*Hyænictis*), which likewise occurs in the Pliocene of India and Europe, the second lower true molar is still retained as a very minute tooth, but the premolars are more like those of existing forms, and the comparatively large $\overline{m.\ 1}$ is placed entirely on the inner side of the carnassial. The muzzle is also comparatively short. In the Indian *H. sivalensis* the first lower premolar is lost, although retained in the European *H. chæretis*. This group forms, indeed, a complete

connection between *Palhyæna* and the next group. In the typical or *Euhyænine* group, as represented by the living Indian Striped Hyæna (*H. striata*) the premolars form blunt cones admirably adapted for crushing large bones. In this group the upper carnassial (fig. 1325) has a short third lobe, while the corresponding

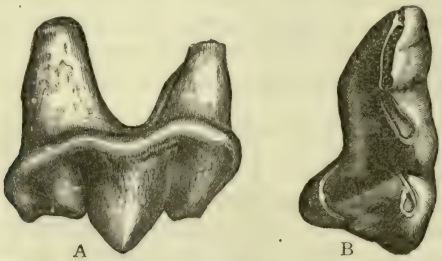


Fig. 1325.—The right upper carnassial tooth of *Hyæna striata*, from the outer (A) and oral (B) aspects; from the Suffolk Crag.

lower tooth still retains its inner cusp and distinct hind talon; but the first lower premolar and second true molar have totally disappeared. Remains referred to the existing species occur in the Suffolk Crag, the caverns of France and the Upper Pliocene or Pleistocene of Italy. *H. arvernensis*, of the Upper Pliocene of

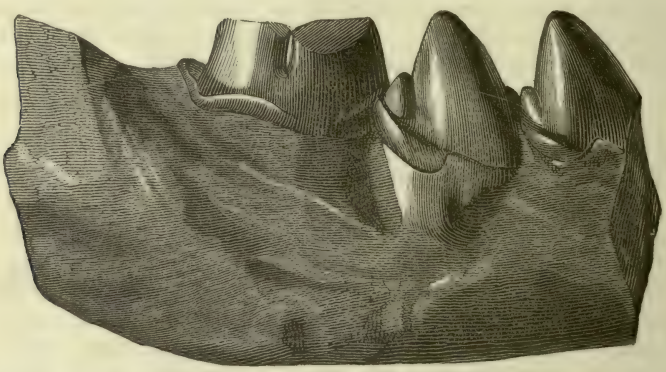


Fig. 1326.—Outer view of hinder part of the right ramus of the mandible of *Hyæna Colvini*; from the Pliocene of India.

France and Italy, seems to be allied to *H. brunnea* of the Cape; while *H. Perrieri* (*topariensis*), of the same deposits makes another step towards *H. crocuta*, having lost the inner cusp to *m.* 1. The most specialised or *Crocutine* group (*Crocuta*) is now represented by the Spotted Hyæna, and is characterised by the long third lobe of

the upper carnassial (fig. 1327, A), and by the loss of the inner cusp and reduction in the size of the hind talon of the lower carnassial (fig. 1327, B).

The most generalised representative of this group is *H. eximia*, of the Lower Pliocene of Greece and Persia, in which the first lower premolar is retained, but the second lower true molar is lost, as in all the other members of this group.[1] *H. Colvini* (fig. 1326) of the

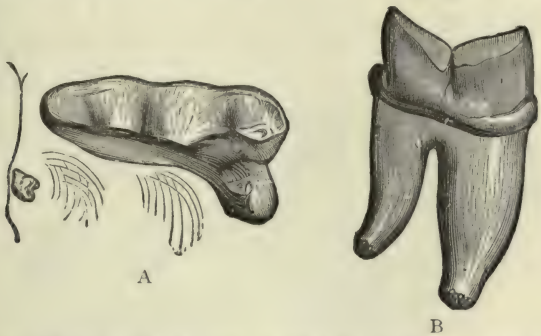


Fig. 1327.—(A), Palatal view of right upper carnassial and true molar; and (B), Outer view of right lower carnassial of *Hyæna crocuta*.

Indian Siwaliks, in which *pm.* 1 has disappeared, may probably be regarded as the ancestor of the existing Spotted Hyæna (*H. crocuta*); while *H. robusta*, of the Upper Pliocene of Italy, is allied to *H. Colvini*, but retains *pm.* 1.

The Spotted Hyæna is now found in South Africa, but occurs in a fossil state in the Pleistocene of both Europe and India. It is characterised by the minute size of the upper true molar (fig. 1327), and the extremely small size of the hind talon of the lower carnassial (*ibid.*) The facial part of the cranium (fig. 1328) is very broad and short.

Remains of the Spotted Hyæna occur in vast quantities in many European cave-deposits; and were especially abundant in the celebrated Kirkdale cave in Yorkshire, explored in the early part of this century by Dean Buckland, and also that of Gailenreuth in Franconia. That these caves were dens in which the Hyænas dwelt is evident from the marks of their teeth on the bones of other animals dragged in by them for food, as well as by other unmistakable evidence.

Family Felidæ.—The *Felidæ*, in which the *Nimravidæ* of Professor Cope are included, are the most specialised representatives of the entire order; this being especially shown in the existing forms by the shortness of the skull, in which there is no alisphenoidal

[1] In a skull of the Spotted Hyæna in the College of Surgeons there is a second lower true molar on one side.

canal, the reduction in the number of the cheek-teeth, the great development of the canines and carnassials, and the digitigrade feet, with their strongly curved and generally perfectly retractile claws, protected by complete bony sheaths. The auditory bulla is greatly inflated, and completely divided by a vertical bony septum. The dental characters common to the entire family are the strong development of the canines, the presence of not more than one upper and two lower true molars, and the circumstance that the three lower incisors are placed in the same horizontal line. With one exception all the known forms have an entepicondylar foramen to

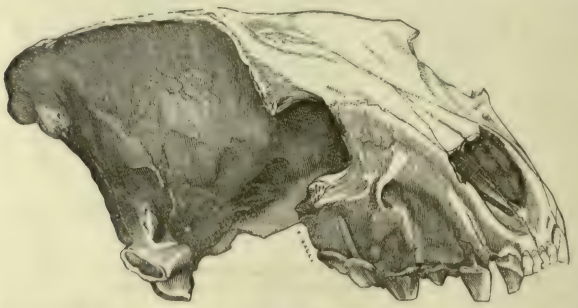


Fig. 1328.—Oblique lateral view of the cranium of *Hyæna crocuta*; from the German Cave. Reduced. (After Owen.)

the humerus. This family was probably derived from the ancestors of the modern *Viverridæ*, the view taken by Dr Schlosser that the true *Felidæ* are directly descended from the Creodonts being very improbable. The earlier forms, constituting the *Nimravidæ* of Professor Cope, present generalised features which are lost in the true Cats.

Here may be mentioned the remarkable genus *Proælurus* from the Lower Miocene and Upper Eocene of France, which includes small Carnivores of generalised affinities, which have been placed by Professor Cope in the true *Felidæ* and by Dr Schlosser in the *Mustelidæ*. The skull agrees with that of *Cryptoprocta* in the possession of an alisphenoidal canal, and the teeth also present resemblances to those of that genus, the formula of the cheek-teeth being *Pm.* $\frac{4}{4}$, *M.* $\frac{1}{2}$. The femur has a third trochanter, and the phalangeals, according to Messrs Scott and Osborn, resemble those of *Dinictis*. This genus also shows signs of affinity with *Palæoprionodon* and *Pseudælurus*.

Dinictis is a somewhat larger but likewise very generalised form, from the Miocene of the United States, which was at one time

classed by Dr Scott with *Cryptoprocta* in a separate family, but is now placed by him in the *Nimravidæ*. The formula of the cheek-teeth is *Pm.* $\frac{3}{3}$, *M.* $\frac{1}{2}$; the upper carnassial has no anterior lobe; the alisphenoid canal is retained; the femur has a third trochanter; the astragalus is flattened and articulates with the cuboid; and the terminal phalangeals, although retractile, are not protected by bony sheaths. Generalised features are also displayed in the base of the skull; and the bones of the skeleton approximate to those of *Cynodictis* and other primitive types.

Of the other generalised forms which may perhaps be included in this family we may mention *Æluropsis* of the Pliocene of the Siwalik Hills, and *Pseudælurus* typically from the Middle Miocene, but recorded by Dr Filhol from the Upper Eocene Phosphorites of France. *Æluropsis* is very imperfectly known, but its mandible seems to approach that of the Machærodonts. Dr Schlosser would include in this genus some of the forms from the French Phosphorites referred

Fig. 1329.—Left lateral aspect of the skull and anterior cervical vertebræ of *Nimravus gomphodus*; from the Miocene of North America. Two-fifths natural size. 3, 4, Premolars; 1, 2, True molars. (After Cope.)

by Dr Filhol to *Proælurus*, and would change the name to *Haplogale*, and place it in the *Mustelidæ*. The typical *Pseudælurus* has three lower premolars, and no inner cusp to the lower carnassial; but in *P. intermedius*, which Dr Schlosser makes the type of the genus *Stenogale*, there were four lower premolars in some instances,

and the lower carnassial retained a small inner cusp. Turning to the consideration of fossil forms which may undoubtedly be included in the present family in the sense in which it is here employed, we find that they have a larger number of teeth than existing forms, and many or all of them retain the alisphenoidal canal. Of these *Ælurictis* (*Ælurogale*) is typically represented by a large species in the Quercy Phosphorites of France, and has also been recorded from the Pliocene of India. The formula of the cheek-teeth is *Pm.* $\frac{3}{(3-4)}$, *M.* $\frac{1}{(1-2)}$; but it is not improbable that this genus may prove inseparable from *Nimravus* (fig. 1329), in which the number of lower premolars is reduced to two. Other allied genera from the North American Miocene are *Archælurus*, with *Pm.* $\frac{3}{(3-4)}$, *M.* $\frac{1}{2}$; *Pogonodon* (fig. 1330), with *Pm.* $\frac{3}{3}$, *M.* $\frac{1}{1}$; and *Hoplophoneus*, with *Pm.* $\frac{(2-3)}{2}$, *M.* $\frac{1}{1}$. In addition to the generally large number of premolars, and the presence of a second lower true molar, this group

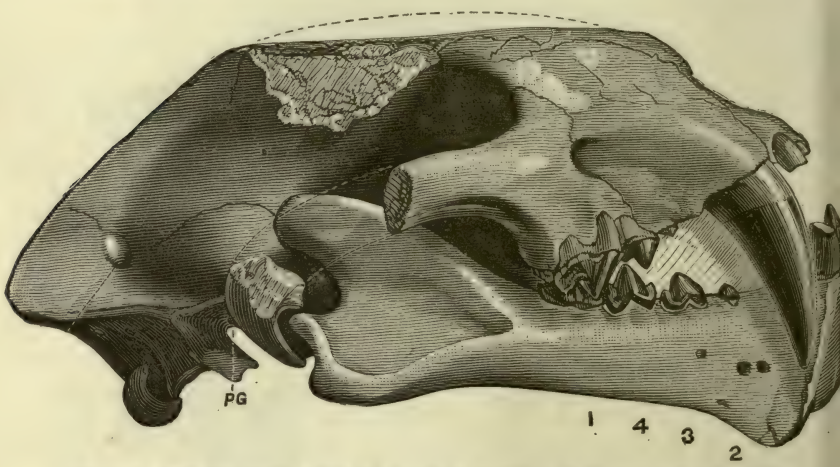


Fig. 1330.—The right lateral aspect of the skull of *Pogonodon platycopis;* from the Miocene of North America. About two-fifths natural size. 2, 3, 4, Premolars; 1, True molar; *PG*, Postglenoid process. (After Cope.)

exhibits the Viverroid feature of a talon, and sometimes an inner cusp (*Hoplophoneus*), to the lower carnassial, and the general absence of the first lobe in the corresponding upper tooth (fig. 1329). In several of the genera the front of the mandibular symphysis is angulated and furnished with a descending flange, as in fig. 1330. In *Hoplophoneus*, of which the entire skeleton has been described by

Messrs Scott and Osborn, the hallux was well developed, there is a distinct line in the scapholunar indicating the boundaries of the scaphoid and lunar, and the femur has a third trochanter; the two last-named features being regarded by the above-mentioned authorities as inherited from a Creodont ancestor.

Turning to the true Cats we have, among existing forms, the Hunting-Leopard of India, forming the genus *Cynælurus*, which is distinguished by its non-retractile claws: it may be represented in the Pliocene of India. All the other "Cats" may be included in the genus *Felis*, although some writers have proposed to split it up into several genera. This genus is spread over the temperate and tropical regions of the greater part of the globe. Although there are five digits in the manus, the hallux of the pes is reduced to a rudiment of its metatarsal; the scapholunar has lost all trace of its primitive duality; and the third trochanter has likewise disappeared from the femur. The dental formula is usually $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{3}{2}$, $M.\frac{1}{1}$; but in some instances there are only two upper premolars, and occasionally there are three lower premolars as an abnormality. The upper carnassial (p^3, fig. 1331) has three

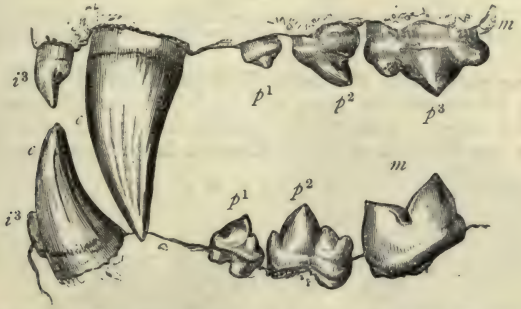


Fig. 1331.—Left lateral view of the dentition of the Lion (*Felis leo*). Reduced. i^3, 3d Incisor; *c*, Canines; p^1-p^3, 2d, 3d, and 4th upper premolars; *m*, True molars; p_1, p_2, 3d and 4th lower premolars.

lobes and a small inner tubercle; while the corresponding lower tooth (*ibid.*, *m*) has no inner cusp or hind talon, although the latter is represented by a minute tubercle in the Lynxes. In Europe this genus makes its first appearance in the Middle Miocene of France, and in North America in the Upper Miocene or Lower Pliocene Loup-Fork beds.

In the Pleistocene of Europe we meet with remains which cannot be distinguished specifically from the existing Lion, although the fossil form has been named *F. spelæa*. Remains of the Leopard (*F. pardus*) also

occur in the Continental cave-deposits ; while in the corresponding deposits of Gibraltar we meet with the Pardine Lynx (*F. pardina*) ; and in those of Bengal we find remains of the Jaguar (*F. onca*) and Ocelot (*F. pardalis*), which now inhabit the same regions. In the Pliocene Siwaliks

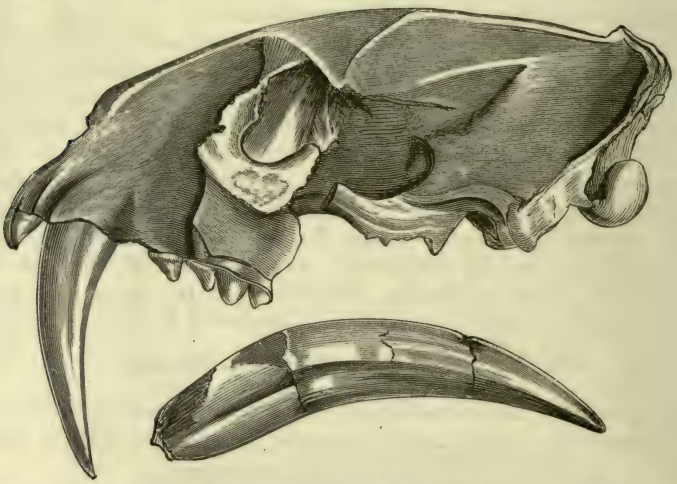


Fig. 1332.—Left lateral view of cranium (A), and larger view of an upper canine (B) of *Machærodus meganthereum ;* from the Upper Pliocene of France. Reduced.

of India we meet with the huge *F. cristata*, which shows characters connecting it both with the Tiger and the Jaguar ; and also smaller forms, one of which appears to have been closely allied to the existing *F. bengalensis*. In the Pliocene of North America large Cats were represented

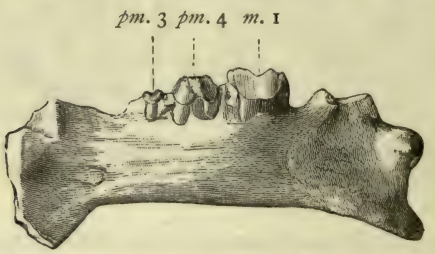


Fig. 1333.—Outer view of the left ramus of the mandible of *Machærodus sivalensis ;* from the Pliocene of India. One-third natural size.

by *F. augusta* and *F. atrox*. In Europe, again, numerous species occur in the Pikermi beds of Greece ; and we may also mention the comparatively small *F. arvernensis* and *F. issiodorensis*, of the French Pliocene, one of which probably also occurred in the corresponding deposits of Persia.

The most remarkable of the true Cats are, however, the extinct Machærodonts or Sabre-toothed Tigers, which are characterised by

the enormous development of the upper canines of the males, by the presence of a deep descending flange in the mandibular symphysis for the protection of the latter, and the angulation of the anterior extremity of this symphysis; the structure of the carnassial teeth being usually of the type of those of the existing Cats. In the type genus *Machærodus* (fig. 1332), which may be taken to include *Smilodon*, *Drepanodon*, and *Trucifelis*, there are three incisors in each jaw; the premolars in the upper jaw never exceed two, and there may be either two or only one of these teeth in the lower jaw; the latter variation occurring in different individuals of a single species. The upper carnassial (fig. 1334) is usually like that of *Felis;* but in the South American *M. neogæus* (fig. 1335) it has four distinct lobes, and is thus the most complex example of this type of tooth that is known. This genus ranges in time from the Quercy Phosphorites to the Pleistocene, and is found in America, Europe, Persia, and India. The South American *M. necator* stands alone among the *Felidæ* in having no foramen to the humerus. The last genus of the family is the curious *Eusmilus*, of the Quercy Phosphorites, in which there are only two incisors and one premolar in the mandible, and the descending flange of the symphysis of the latter is of enormous depth. The existence of this extremely specialised form at such an early epoch is noteworthy; not less so being the total extinction of the Machærodonts, which, it has been suggested, may be due to their excessive specialisation having rendered them incapable of obtaining their subsistence.

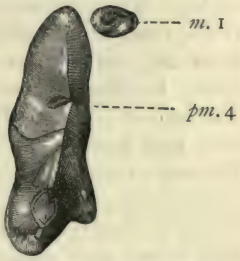


Fig. 1334.—Oral aspect of the left upper carnassial and true molar of *Machærodus sivalensis;* from the Pliocene of India.

Fig. 1335.—Right lateral view of the skull of *Machærodus neogæus;* from the Pleistocene of South America. Greatly reduced.

Suborder 3. Creodonta. — The members of the suborder Creodonta (or Carnivora Primigenia) are all extinct, and their serial position has led to much discussion. By some authorities they have been classed with the Polyprotodont Marsupials; from which, however, they differ by the presence of a complete milk-den-

tition, by the reduced number of incisors, and the absence of the inflection of the angle of the mandible, and of palatal vacuities. By others they have been regarded as closely allied to certain families of the Insectivora, and, together with the latter, are classed as a section of a large and ill-defined order termed the Bunotheria; while a third writer ranks them as an order of equal value with the existing Insectivora and Carnivora. Their relationship appears, however, on the whole, to be decidedly nearest to the true Carnivora, and they are accordingly here classed as a division of that order. They undoubtedly, however, exhibit affinities to the Insectivora, from which they are distinguished by the Carnivorous type of their incisors and canines; while the remarkable resemblance existing between their cheek-teeth and those of the Polyprotodont Marsupials is probably indicative of a distinct genetic relationship with that group. Mention has already been made of their resemblances to the Condylarthrous Ungulates.

The following are the chief characters of this suborder: The brain is of relatively small size; the fourth upper premolar and the first lower true molar are not differentiated as an opposed pair of carnassials, but resemble more or less closely the tooth immediately behind or in front of them, which is either conical or of a more or less secant type; and the upper true molars are either subtriangular or simply secant. The tibial face of the astragalus is, moreover, generally devoid of a groove; the scaphoid and lunar are usually separate; the femur has a third trochanter; and the feet were plantigrade. In all cases where there is the full number of incisors, the second pair in the lower jaw is thrust up above the other two, as in so many of the Carnivora Vera. The structure of the cranium approximates to that of *Amphicyon*.

Family Hyænodontidæ.—This family includes the most specialised forms. The dentition (fig. 1336) is of a markedly sectorial type, the inner tubercle of the hinder upper cheek-teeth being very small; and there is no inner cusp to the lower true molars. In the type genus the scaphoid and lunar of the carpus were united. *Hyænodon* has the dental formula $I.\ \frac{3}{3}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{4}{4}$, $M.\ \frac{2}{3}$; the inner tubercle of the two upper true molars is almost wanting, and the third lower true molar differs from the two teeth in front (fig. 1336), and somewhat resembles the carnassial of *Felis*. This genus includes species varying in size from a Leopard (*H. horridus*) to a small Fox (*H. vulpinus*), and is widely distributed both in time and space. Thus it is found in Europe, and also in North America, where it ranges from the Upper Eocene to the Lower Miocene; while in India it survived into the Pliocene. One species has been found in the Upper Eocene of Hampshire. The species from the

Upper Miocene of North America is remarkable as being the only known Mammal, except certain Edentates and Cetaceans, in which the pterygoids unite beneath the nasal passage. One of the European forms was originally described as *Taxotherium*. In the allied *Pterodon*, which, together with *Oxhyæna*, some writers refer to a distinct family, the third upper true molar is present, and has a

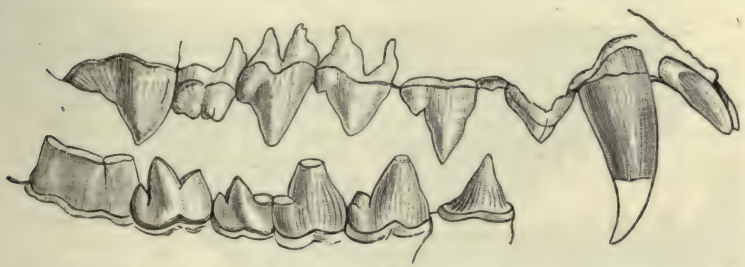


Fig. 1336.—Right lateral aspect of the dentition of *Hyænodon horridus*, wanting the teeth in advance of the second lower premolar; from the Miocene of North America. Reduced. (After Leidy.)

transversely elongated crown; there may be either two or three upper incisors, and the first lower premolar is sometimes absent. The first and second upper true molars differ from those of *Hyænodon* by the large size of their inner tubercle, and the last true molar is like the second; the cranium in many respects resembles that of *Amphicyon*. This genus is represented by

Fig. 1337.—The left side of the anterior half of the palate of *Oxhyæna gallicæ*: from the French Phosphorites.

three comparatively large species from the Upper Eocene (Lower Oligocene) of Europe. An allied form, from the French Phosphorites, has been named *Pseudopterodon*, and connects the former genus with *Theuritherium*. The remarkable genus *Oxhyæna*, of the North American Eocene and the French Phosphorites, has an elongated mandibular symphysis, with the dental formula $I. \frac{(2-3)}{0}$, $C. \frac{1}{1}$, $Pm. \frac{4}{4}$, $M. \frac{2}{2}$; the species figured in the woodcut having only

two upper incisors. *Protopsalis* is another Eocene American genus; while *Hemipsalodon*, from the White River Miocene of Canada, is the largest form yet known in the suborder, and has the full typical Eutherian dentition.

Family Proviverridæ.—The members of this family (fig. 1338) are characterised by the large size of the inner tubercle of the upper

Fig. 1338.—Skull (*a*, *b*, *c*) and tarsus (*d*) of *Proviverra Whitiæ*; from the Wasatch Eocene of Wyoming, U.S.A. Two-thirds natural size.

true molars, and by the presence of an inner cusp to the blade of those of the lower jaw. The type genus *Proviverra* (*Cynohyænodon* or *Stypolophus*) occurs in the Upper Eocene of both Europe and North America; one of the European forms being from the Quercy Phosphorites. The skull (fig. 1338) is elongated, and the lower true

molars, which are differentiated into a blade and a hinder tubercular talon, closely resemble the lower carnassial of *Dasyurus* (fig. 1145) among the Marsupials, and of *Cynodictis* and *Viverra* in the Carnivora Vera, and thus indicate how the latter group has in all probability been derived from a form allied to the present family; the hinder lower molars of the Carnivora Vera having become tubercular and non-secant. Other members of this family found in the Lower, or Puerco, Eocene of North America are *Deltatherium*, *Chriacus*, and, according to Professor Cope, *Mioclænus*, and probably *Triïsodon* and *Onychodectes*. *Didelphodus*, from the higher Eocene of America, may also be placed here, as well as *Quercytherium*, from the French Phosphorites, and perhaps *Galethylax*, of the Paris Eocene. *Conoryctes* and *Hemiganus* are allied Puerco types; the latter being distinguished by the fusion of the roots of the upper true molars, and hence regarded by Professor Cope as the type of a distinct family showing signs of affinity with the Tillodontia.

Family Arctocyonidæ.—This family is typified by the genus *Arctocyon*, of the Lower Eocene of France, with which may be classed *Hyodectes* and *Heteroborus*, of the Lower Eocene of Rheims. Dr Schlosser suggests that *Mioclænus* should come in this family.

Family Mesonychidæ.—The members of this family are short-jawed forms, usually having the typical number of teeth, which are less different than in the other families from those of the Carnivora Vera. The type genus *Mesonyx*, from the North American Eocene, has a grooved astragalus; and other genera which are referred to this family are *Dissacus*, *Sarcothraustes*, and *Patriofelis*, from the latter area, and not improbably *Theuritherium*, of the French Phosphorites. *Dissacus* has, however, no trochlea to the astragalus, and is therefore nearer to the *Proviverridæ*. *Amblyctonus*, of the North American Eocene, is an allied form with the astragalus not grooved, on which account it has been regarded as the type of a distinct family. *Palæonictis*, of the Lower Eocene of France, may be allied.

Family Uncertain.—A few genera cannot at present be definitely placed. These comprise *Thylacomorphus*, from the French Phosphorites, which it has been suggested may be identical with *Proviverra;* and *Dasyurodon*, or *Apterodon*, from the Lower Miocene (Middle Oligocene) of Flonheim, which Dr Schlosser thinks may turn out to be the same as *Oxhyæna galliæ*. *Dromocyon*, of the Bridger Eocene, is not improbably founded upon a very old individual of *Mesonyx;* while the imperfectly known *Argillotherium*, from the London Clay, may prove to be identical with one of the American genera. Finally, it should be mentioned that Dr Schlosser would place in this suborder the genus *Platychœrops*, which is here classed with the Tillodontia.

CHAPTER LXIII.

CLASS MAMMALIA—continued.

Orders Insectivora, Chiroptera, and Primates.

Order IX. Insectivora.—The Insectivora are a group of small Mammals, not very readily defined from the characters of their bones and teeth. The teeth are well developed, and generally easily separable into the usual four divisions, although in certain cases the distinction between incisors, canines, and premolars is not very clear. The dentition is diphyodont and heterodont; the cheek-teeth are always rooted, and their crowns carry a number of minute pointed cusps; the crowns of the upper true molars being either subquadrangular or triangular in shape. The first pair of incisors in some cases are not in contact in the middle line; and the canines are often weak. The zygomatic arches of the skull are usually either weak or entirely absent; clavicles are present in all existing forms except *Potamogale;* in the carpus the scaphoid and lunar are separate; the feet are usually either entirely or partially plantigrade, and their digits are generally five in number, with the terminal phalangeals unguiculate, narrow, and subcylindrical. Certain Insectivores, such as the Moles and *Galeopithecus*, are remarkable as being the only Mammals in which ossified vertebral intercentra are known to have been developed in the dorso-lumbar region. As a rule the humerus has a foramen.

Fossil forms apparently indicate a relationship on the one hand with the Creodont Carnivora, and on the other with the Lemuroid Primates; those genera with square-crowned upper true molars approximating to the latter group, while those in which the crowns of these teeth are triangular show the nearest affinity to the former. Dr Schlosser concludes, with great probability, that the Lemuroids, Insectivores, and Creodonts are all diverging branches from a common stock, which may also have given origin to the Condy-

larthrous Ungulates. The resemblance of the molars of *Tupaia* to those of the Marsupial genus *Perameles*, and that between the same teeth in the Creodonts and the *Dasyuridæ*, further suggests the connection of this common stock with the ancestral types of the Polyprotodont Marsupials.[1] The Insectivores agree with the Lemuroids not only in dental characters, but also in the presence of clavicles, in their plantigrade feet, and the discoidal placenta; and it is indeed quite evident that the ancestral stock of the Primates must have been provided with complete clavicles.

This order may be divided into the suborders Insectivora Vera and Dermoptera. The former may be further subdivided into two sections, in the first of which the molars have broad and squared crowns, with their cusps frequently arranged like the letter W, while in the second section the crowns of these teeth are narrow and V-shaped, with the apex of the V directed inwardly (tritubercular). The Dermoptera, represented only by the volant genus *Galeopithecus*, are unknown in a fossil condition. It should, however, be observed that this genus, although not on the direct line of descent, indicates the manner in which the Insectivores have become modified into the Bats. The first section of the Insectivora Vera comprises the existing *Tupaiidæ*, *Macroscelididæ*, *Erinaceidæ*, *Soricidæ*, and *Talpidæ*, together with the extinct *Microchœridæ* and *Dimylidæ*.

Family Tupaiidæ.—The Tupaias are small arboreal Insectivores confined at the present day to the Indo-Malayan region. The genus *Parasorex*, from the Middle Miocene of the Continent, has the dental formula $I.\frac{3}{3}$, $C.\frac{1}{1}$, $Pm.\frac{4}{4}$, $M.\frac{3}{3}$, and may be provisionally placed in this family, although, according to Dr Schlosser, it approximates in several respects to the *Macroscelididæ*. There is one more upper incisor and one more premolar in each jaw than in *Tupaia*, and the last two premolars are somewhat more complex. The above-mentioned writer regards this genus as the representative of a group connecting the *Tupaiidæ* of Asia with the *Macroscelididæ* of Africa. An Insectivore from the Middle Miocene of Sansan, described as *Lantanotherium*, is said to be very nearly allied to *Tupaia*.

Family Erinaceidæ.—Since the *Macroscelididæ* are at present unknown in a fossil state, we may pass to the *Erinaceidæ* or Hedgehogs. In the typical genus *Erinaceus* (fig. 1339) the dental formula is $I.\frac{3}{2}$, $C.\frac{1}{1}$, $Pm.\frac{3}{2}$, $M.\frac{3}{3}$; the first pair of upper incisors are large,

[1] On embryological grounds some authorities are disposed to regard the Marsupials as being off the line of Eutherian ancestry; but it must be borne in mind that the evidence only includes existing types.

and separated from one another by a space, the five succeeding teeth small and conical, the last premolar and the two first true molars broad and cusped, while the last tooth is very small; and there is a vacuity on either side of the hinder part of the palate. The existing *E. europæus* has been found fossil in the Pleistocene; a small species occurs in the Upper Miocene of Œningen, in Switzer-

Fig. 1339.—Left lateral view of the skull of the Hedgehog (*Erinaceus europæus*).

land, and others are found in the Middle Miocene of France. In the Lower Miocene of the same country occurs the genus *Palæoerinaceus*, distinguished from *Erinaceus* by the absence of vacuities in the palate, and the greater relative width of the latter. An apparently allied form from the French Miocene has been described by Gervais under the name of *Erinaceus arvernensis*, which is, however, not the same as *E. arvernensis* of De Blainville. From the Quercy Phosphorites there have been obtained remains of other members of this family more nearly allied to the existing *Gymnura* of Madagascar, but presenting characters which also link them very closely with *Erinaceus* through *Palæoerinaceus*. These Quercy forms have been referred to three genera under the names of *Neurogymnurus*, *Cayluxotherium*, and *Comphotherium*, but it appears probable that the second is a synonym of the first. The teeth of *Neurogymnurus* and *Cayluxotherium* are like those of *Gymnura*, but the palate has vacuities as in *Erinaceus*; *Comphotherium* is distinguished by a cingulum to the lower true molars, which also occurs in *Gymnura*. *Neurogymnurus* has also been recorded from the Upper Eocene of Hampshire.

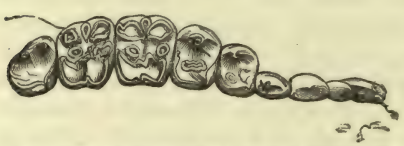


Fig. 1340.—Palatal view of the right upper cheek-dentition of *Microchœrus erinaceus*; from the Upper Eocene of Hordwell.

Family Microchœridæ.—The genus *Microchœrus* (fig. 1340), from the Upper Eocene of Hordwell, with which *Heterohyus*, of the corresponding beds of France, may be identical, agrees with *Erinaceus* in showing an interval between the first upper incisors of either side, and may be provisionally placed in this order. It has

been regarded as allied to the Lemuroid *Hyopsodus*, but Professor Osborn states that it is really very different. The dental formula may be given approximately as *I.* $\frac{2}{?}$, *C.* $\frac{1}{1}$, *Pm.* $\frac{3}{?}$, *M.* $\frac{3}{3}$. The two upper incisors have compressed crowns, somewhat like those of the two succeeding teeth; but the last two premolars and the true molars have broad and flat crowns, carrying a number of small cusps.

Family Dimylidæ.—This family is proposed by Dr Schlosser for the genera *Dimylus* and *Cordylodon;* two minute Insectivores from the European Miocene which appear to be related to the *Erinaceidæ*.

Family Soricidæ.—The *Soricidæ*, or Shrews, are readily characterised by their dentition, in which the first upper incisor is large and furnished with a basal tubercle, while between it and the last premolar there are a variable number of small incisors and premolars, together with the equally minute canine. In the mandible the number of teeth is always *I.* 1, *C.* 1, *Pm.* 1, *M.* 3; the incisor being proclivous and much produced forwards, and the canine the smallest tooth of the series. Existing species of *Sorex*, and perhaps of *Crossopus*, occur in the Norfolk Forest-bed, while a species of the former genus, regarded as extinct, has been recorded from the Pleistocene breccias of Sardinia. Existing species of *Sorex* or *Crocidura* also occur in the caverns of Madras. Numerous forms have been recorded from the Continental Tertiaries, ranging from the Miocene to the Quercy Phosphorites, some of which are referred to *Sorex*, while others, such as the Quercy species, have been regarded as generically distinct, and named *Amphisorex*. Dr Schlosser thinks that *Orthaspidotherium* and *Pleuraspidotherium*, mentioned on p. 1288, might be placed here.

Family Talpidæ.—The *Talpidæ*, or Moles and Desmans, are closely allied to the *Soricidæ*, although easily distinguished by the non-production of the first lower incisor; they are usually of fossorial, but in some cases are of natatorial habits. This family is divided into the *Myogalinæ* and the *Talpinæ;* in the former the humerus and clavicle being moderately elongated. In this subfamily the aquatic type genus *Myogale*, in which the dentition (fig. 1341) is *I.* $\frac{3}{3}$, *C.* $\frac{1}{1}$, *Pm.* $\frac{4}{4}$, *M.* $\frac{3}{3}$, is represented in the Norfolk Forest-bed by the existing Desman (*M. moschata*), of the rivers of Russia; the fossil form having been originally described under the name of *Palæospalax*. Remains of this genus have also been obtained from the Middle and Lower Miocene of France. *Tetracus*, from the Lower Miocene of Ronzon, near Puy-en-Velay, is a small Insectivore apparently presenting affinities both with *Myogale* and *Erinaceus;* and allied to this genus are two other imperfectly known

forms from the French Lower Miocene, to which the names *Echinogale* and *Mysarachne* have been applied. These genera, and perhaps the following one, seem to show indications of a transition between the existing members of the *Erinaceidæ*, *Soricidæ*, and *Talpidæ;* and thus, together with the imperfect nature of the remains by which they are known, render the determination of their serial position a matter of great difficulty. The French Lower Miocene has also yielded the allied genus *Plesiosorex* (fig. 1342), which appears to have belonged to the present subfamily, but is only known by the mandible, in which there are ten teeth. The smaller *Amphidozotherium*, from the Quercy Phosphorites, is said to be allied to the existing fossorial genus *Urotrichus* of Japan and North America. In the second subfamily, or *Talpinæ*, in which the humerus and clavicle are of enormous relative breadth, the typical genus *Talpa* (fig. 1343) has the same dental formula as in *Myogale*. The common Mole, *T. europæa*, occurs fossil in the Norfolk Forest-bed, while a species from the Pleistocene breccia of Sardinia is regarded as peculiar, and named *T. tyrrhenaica*. The genus itself is apparently as old as the Lower Miocene, although the species (*T. telluris*) from the middle stage of that period has been distinguished by some writers as *Hyporyssus*, and the one from the lower stage (*T. acutidens*) as *Geotrypus*.[1] The Quercy Phosphorites have yielded a very closely allied form, which is, however, regarded by its describer as generically distinct, and named *Protalpa cadurcensis*. From the Eocene of North America an allied genus has been described under the name of *Talpavus;* but the so-called *Herpetotherium*, of the Miocene of the same country, which has been regarded as related to the Moles, is referred to *Didelphys* (fig. 1151, p. 1281).

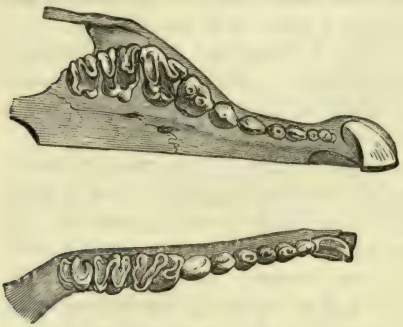


Fig. 1341.—Palatal view of right upper and lower dentition of *Myogale moschata*. Europe.

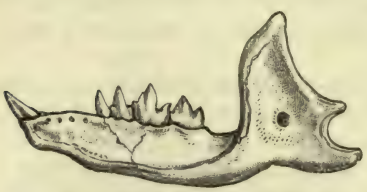


Fig. 1342.—Left ramus of lower jaw of *Plesiosorex soricinoides*, wanting the last true molar and the teeth between the first incisor and the fourth premolar; from the Lower Miocene of the Auvergne. Twice natural size. (After De Blainville.)

[1] Preoccupied by *Geotrupes* in the Coleoptera.

Family Adiposoricidæ.—This family contains the minute *Adiposorex* and *Adiposoriculus*, from the Lowest Eocene of Rheims, which Dr Schlosser regards as related to the Shrews, but forming a distinct family, attaining a higher degree of development.

Family Leptictidæ (Ictopsidæ).—The second section of the Insectivora Vera includes the recent families *Potamogalidæ*, *Solenodontidæ*, *Centetidæ*, and *Chrysochloridæ;* and we may provisionally place in the same neighbourhood the family *Leptictidæ* of the North American Eocene and Miocene. The latter forms are regarded by Dr Schlosser as true Insectivora, although they were placed by Professor Cope near the *Hyænodontidæ*. The family includes the genera *Leptictis*, *Mesodectes*, *Ictops*, and perhaps *Geolabis*.

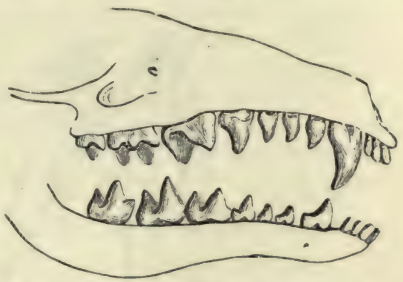


Fig. 1343.—Lateral view of right dentition of the Mole (*Talpa europæa*). Enlarged.

Finally the names *Centetodon*, *Entomodon*, *Entomacodon*, *Centracodon*, and others have been applied to the remains of small entomophagous mammals from the Lower Tertiaries, of which the serial position is doubtful.

Order X. Chiroptera.—The Chiroptera are characterised by the fact that the anterior limbs are longer than the posterior, the digits of the fore limb, with the exception of the pollex, being enormously elongated (fig. 1344). These elongated fingers are united by an expanded membrane or patagium, which is also extended between the fore and hind limbs and the sides of the body, and in many cases passes also between the hind limbs and the tail. The patagium thus formed is naked, or nearly so, on both sides, and serves for flight. In the manus the pollex, and sometimes the next digit as well, is unguiculate, or furnished with a claw; but the other digits are destitute of nails. In the hind limbs all the toes are unguiculate, and the hallux is not in any respect different from the other digits. Well-developed clavicles are always present, and the radius has no power of rotation upon the ulna. The four kinds of teeth are always present (although the molars are aborted in *Desmodus*), and the dental formula is never known to exceed

$$I.\ \frac{2}{3},\ C.\ \frac{1}{1},\ Pm.\ \frac{3}{3},\ M.\ \frac{3}{3}.$$

This order, which is evidently a branch from the Insectivorous stock, is divided into the suborders Megachiroptera and Microchiroptera. The former, which is characterised by the possession of smooth cheek-teeth, marked by a longitudinal groove, comprises

the *Pteropodidæ*, or Fruit-bats, and is unknown in a fossil condition. In the latter, which comprises all other Bats, the teeth are covered with minute pointed cusps; nearly all the species being of comparatively small size. The most remarkable feature presented in the past history of this order is the occurrence of forms closely

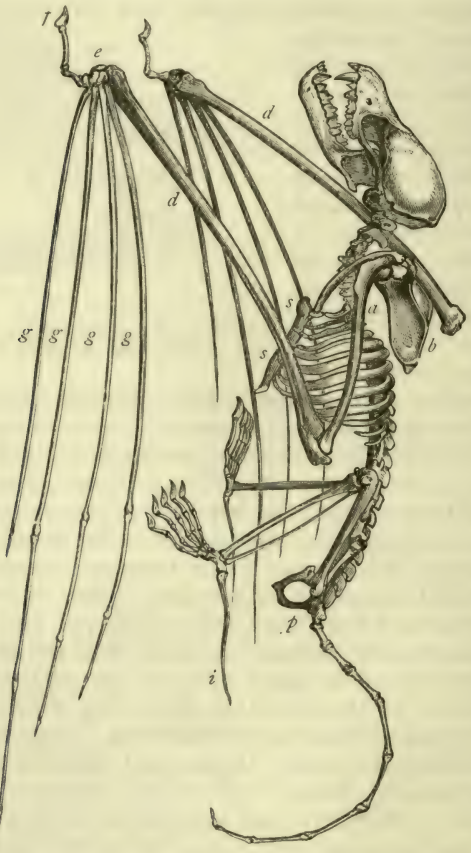


Fig. 1344.—Skeleton of the Mouse-coloured Bat (*Vespertilio murinus*). *a*, Humerus; *b*, Scapula; *d*, Radius, with the rudimentary ulna at its proximal end; *e*, Carpus; *f*, Pollex; *g g*, Metacarpals; *s s*, Sternum; *p*, Pelvis; *i*, Supplementary bone attached to the calcaneum.

allied to those of the present day as low down as the Bridger Eocene of North America, which indicates that the characteristic features of the order were probably acquired at a period not later than the Lower Eocene or Cretaceous epoch. The following families of *Microchiroptera* may be noticed :—

Family Rhinolophidæ.—In the existing genera of this family the dental formula never exceeds $I.\frac{1}{2}$, $C.\frac{1}{1}$, $Pm.\frac{2}{3}$, $M.\frac{3}{3}$, and the nose carries a peculiar leaf-like expansion. The type genus *Rhinolophus*, in which the dental formula is as above, is represented in the cave-deposits of Europe by remains of existing species. Two Bats, from the Upper Eocene Phosphorites of France, have been referred to this genus under the names of *R. dubius* and *R. antiquus*, but the latter species is regarded by some authorities as entitled to generic distinction, and the term *Pseudorhinolophus* has accordingly been proposed for its reception. *Alastor*, from the same deposits, is an extinct genus characterised by the extreme shortness of the nasal region and other features of the skull. *Palæonycteris*, from the Lower Miocene of France, is stated to be allied to *Rhinolophus*, but the premolars are $\frac{3}{3}$, and the limb-bones are said to resemble those of the South American *Molossus*. *Phyllorhina*, in which the premolars are $\frac{(1-2)}{2}$, is represented by the living oriental *P. diadema* in the Pleistocene cave-deposits of Madras, and perhaps by a species in the Quercy Phosphorites.

Family Vespertilionidæ.—In the *Vespertilionidæ* the nose does not carry a distinct follicular appendage, the number of incisors is usually $\frac{(1-2)}{3}$, and in some genera there are three premolars in each jaw. Of *Plecotus*, the existing *P. auritus* occurs in the cavern-deposits of Europe. *Vesperugo*, with incisors usually $\frac{2}{3}$, and premolars $\frac{2}{2}$, is perhaps represented in the Upper Eocene of the Paris basin by the well-known *V. parisiensis*, which appears closely allied to the existing *V. serotina*, although generically separated by some writers under the name of *Nyctitherium*. This genus has also been described from the Eocene of North America, where it is represented by several species, ranging as low down as the Bridger horizon, some of which have been described under the name of *Nyctitherium*. *Nyctilestes serotinus*, from the same deposits, is the type of an allied genus. Remains of the existing *V. noctula* (fig. 1345) occur in the English Pleistocene. In the type genus *Vespertilio* the dental formula is $I.\frac{2}{3}$, $C.\frac{1}{1}$, $Pm.\frac{3}{3}$, $M.\frac{3}{3}$. The existing *V. murinus* occurs in the cave-deposits of France, and a considerable number of species have been referred to this genus from the Middle Tertiaries of the Continent, but the generic reference must be con-

sidered in some instances as open to doubt. Among these may be mentioned *V. murinoides*, from the Middle Miocene of France, and *V. precox* and *V. insignis*, from the Lower Miocene of Germany. A Bat from the Quercy Phosphorites originally named *V. Bourguignati* has been made the type of a distinct genus *Vespertiliavus*,

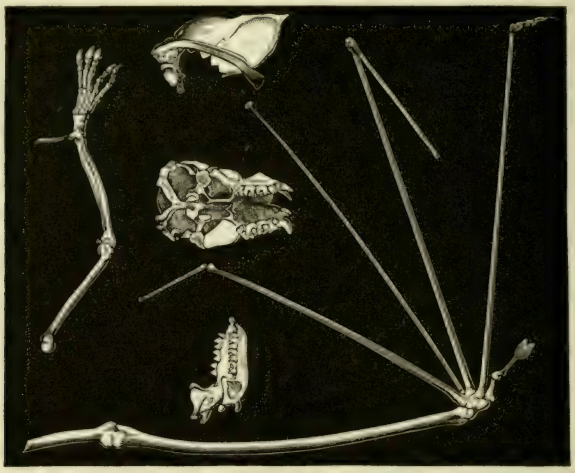


Fig. 1345.—*Vesperugo noctula*.[1] Skull, scapula, and fore and hind limbs; from a fissure in the Mendip Hills.

and differs from *Vespertilio* in the proportions of the premolars. Remains of numerous existing members of this family have been recorded from European caverns.

Family Emballonuridæ.—This is an extensive family showing great variation in the number of the teeth, and mainly characterised by the nose and muzzle being devoid of expansions, and by certain peculiar features connected with the tail. All its members at the present day are confined to tropical and subtropical regions. In *Taphozous*, of which the dental formula is $I.\frac{1}{2}$, $C.\frac{1}{1}$, $Pm.\frac{2}{2}$, $M.\frac{3}{3}$, remains of the existing *T. saccolæmus* occur in the cave-deposits of Madras; and Dr Weithofer considers that certain humeri from the Quercy Phosphorites may indicate the occurrence of this genus in the Upper Eocene. In the Brazilian cave-deposits we meet with remains of a *Molossus* (*Dysopes*), probably identical with the living *M. Temmincki* of the same region.

Family Phyllostomatidæ.—The last family is that of the *Phyl-*

[1] In the previous edition this figure was wrongly named *V. parisiensis*.

lostomatidæ, now confined to tropical America, and distinguished by the presence of cutaneous expansions in the nasal region, as well as by a peculiarity in the number of the digits of the manus. In this family the existing *Vampyrus spectrum*, having the dental formula $I.\ \frac{2}{2}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{2}{3}$, $M.\ \frac{3}{3}$, together with several undetermined species of *Phyllostoma* (fig. 1346), in which the premolars are $\frac{2}{2}$, occur in the cave-deposits of Brazil. Curiously enough the mandible of a large Bat, from the Quercy Phosphorites, described under the name of *Necromantis*, appears to indicate the occurrence of this family in the European Eocene.

Fig. 1346.—Lateral view of the skull of the Javelin Bat (*Phyllostoma hastatum*).

In conclusion it should be observed that Professor Cope thinks that a small Mammal from the Miocene of North America, which he has described under the name of *Domnina*, may possibly belong to the Chiroptera.

Order XI. Primates.—This, the highest order of Mammals, comprises the Lemurs, Monkeys, Baboons, Apes, and Man. The digits are unguiculate, and usually five in number; and in existing forms, with the exception of Man, the hallux is opposable to the other digits. The pollex may be wanting, but when present is usually opposable to the other digits of the manus. The dentition is diphyodont and heterodont. In the existing and the allied extinct genera the incisors are usually $\frac{2}{2}$, and the true molars (with the exception of the *Hapalidæ*) $\frac{3}{3}$ in number. The crowns of the cheek-teeth are, moreover, always adapted for grinding, and those of the true molars generally consist of four tubercles, or cusps, which may either be simple, or modified so as to form imperfect transverse ridges or crescents; but some extinct types have tritubercular upper molars.

The structure of the premolars is always simpler than that of the true molars; and in many Lemuroids the anterior lower premolar assumes the form and functions of a canine, as in the *Cotylopidæ* (fig. 1347). All existing forms have the orbit entirely surrounded by bone; while complete clavicles are present, and there is

no entepicondylar foramen to the humerus, nor a third trochanter to the femur. The terminal phalangeals of the digits are flattened. In the soft parts there is a discoidal placenta, as in the Insectivora.

In our present state of knowledge, it is difficult to draw a line between the more generalised fossil representatives of this order and the Insectivora. Some remarks on the probable origin of the Primates have been already made under the head of the last-named order, while others are added below.

Suborder 1. Lemuroidea.—The existing members of this group differ in many respects from the following suborder, but attention may be directed mainly to certain osteological and dental characters. Thus the skull (fig. 1347) has a somewhat produced muzzle; the orbits are not closed behind by bone, but open freely beneath the post-orbital bar into the temporal fossa; and the lachrymal foramen is situated on the outer surface of the skull, instead of within the orbit. The nostrils have a peculiar twist on the outer side. The incisors vary much in the different families, but they are frequently separated in the middle line, and are usually $\frac{2}{2}$ in number, although they are reduced to $\frac{1}{1}$ in *Chiromys;* those of the lower jaw being frequently procumbent. Canines are present except in *Chiromys*. The number of premolars varies from $\frac{1}{0}$ in *Chiromys* to $\frac{4}{4}$ in the extinct *Adapis*, but is generally either $\frac{2}{2}$ or $\frac{3}{3}$; while frequently the second lower premolar is larger than either of the following teeth. The outer tubercles of the upper true molars (fig. 1349) are laterally flattened, while the inner ones form imperfect crescents; and in the lower molars the tubercles likewise form a pair of imperfect crescents. The second digit of the pes has a long claw-like nail, but all the other digits have nails; the digits themselves being five in number, and the long pollex being generally opposable. The brain has but few convolutions, and the cerebellum is only partially covered by the cerebrum.

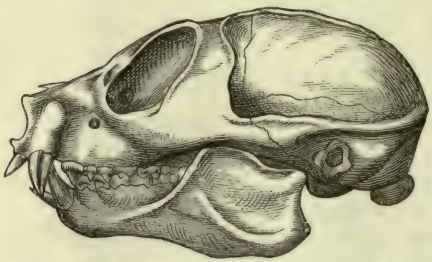


Fig. 1347.—Left lateral aspect of the skull of the Slow Loris (*Nycticebus tardigradus*); from the Malayan region. The tusk-like tooth in the lower jaw is the second premolar. (After Giebel.)

Many of the foregoing characters are common to other orders,

such as the Insectivora. In the case of fossil forms it appears, indeed, that the Lemuroids can only be distinguished from the Insectivores by the absence of the cleft in the terminal phalangeals of the digits, so that when these are unknown it is frequently very difficult, if not impossible, to determine to which order such forms should be referred. Since, moreover, as we have stated under the head of the Insectivora, it is probable that Insectivores and Lemuroids are descended from the same ancestral stock we must expect to find the characters common to the two groups increasing in importance and number as we recede in time. By Professor Cope the Lemuroids are, however, regarded as closely allied to the Condylarthrous Ungulates; and that writer proposes to brigade together the Primates, Condylarthra, and Hyracoidea under the common name of Taxeopoda; the Condylarthra being regarded as the ancestral type. Now although we may be prepared to admit the derivation of the Condylarthra from the common stock which gave origin to the Insectivora and Primates (see p. 1455), yet the apparent absence of clavicles in all the known representatives of that group renders it at least premature to say definitely that it gave rise to the Primates. At the present day Lemuroids are confined to the warmer regions of the Old World, being especially characteristic of Madagascar and certain parts of Africa. The recent forms are divided into the families *Lemuridæ*, *Tarsiidæ*, and *Chiromyidæ*.

Family Hyopsodontidæ.—This family name was proposed by Dr Schlosser[1] for the reception of certain North American Eocene forms now looked upon by most writers as undoubted Lemuroids, although some of them have been classed among the Insectivora. The most generalised form is *Pelycodus*, from the Eocene of New Mexico, at one time regarded by Professor Cope as an Insectivore allied to *Tupaia*. Dr Schlosser states that it presents some affinity to the Insectivorous *Microchœrus*, which he places in the same family. *Hyopsodus* (fig. 1348), of the American Eocene, has the dental formula $I.\frac{2}{2}$, $C.\frac{1}{1}$, $Pm.\frac{4}{4}$, $M.\frac{3}{3}$; the third upper premolar is as well developed as the second, by which character it is readily distinguished from *Microchœrus*, to which it has been compared. Several species have been described, of which one comes from the Lower or Puerco Eocene, while the others are from the higher Wasatch and Bridger horizons. *Microsyops* is

Fig. 1348.—Palatal view of the left upper (*a*) and lower (*b*) dentition of *Hyopsodus vicarius*; from the Eocene of North America. (After Cope.)

[1] Wrongly given as *Hyopsodidæ*.

an apparently allied form from the North American Eocene said to have only three premolars. In *Pelycodus* the hallux was not opposable. There are a number of other names which have been applied to American forms of uncertain position, but since the synonymy is very complex nothing would be gained by quoting them here.

Family Lemuridæ.—Passing to Lemuroids more closely allied to existing forms those extinct genera may first be noticed many of which exhibit the generalised feature of having four premolars in either jaw, on which grounds, coupled with certain slight differences in the form of the lower premolars, Dr Schlosser regards them as constituting a distinct family—the *Adapidæ*. We may, however, provisionally follow Professor Flower in including them in the *Lemuridæ*, of which they will form the subfamily *Adapinæ*. The best known of these forms is the type genus *Adapis* (*Aphelotherium*, or *Palæolemur*), from the Upper Eocene (Oligocene) of both France and England, in which the dental formula is $I.\frac{2}{2}$, $C.\frac{1}{1}$, $Pm.\frac{4}{4}$, $M.\frac{3}{3}$; the upper molars being of a quadritubercular type. The last upper premolar is as complex as the true molars, which (fig. 1349) resemble those of *Lepidolemur* and *Hapalemur*, while the skull makes the nearest approach to that of *Propithecus*. It has, indeed, been suggested that this and the allied genera show certain relationships to the Anthropoidea which are not seen in existing representatives of the suborder; but their alleged relationship to the bunodont Artiodactyla does not appear to be substantiated. The imperfectly known genus *Cænopithecus* from the Upper Eocene of Switzerland is regarded by Dr Schlosser as identical with *Adapis*, although Professor Rütimeyer considers that it is allied to the American *Pelycodus*. From the Eocene of North America we have the two nearly related genera *Tomitherium* and *Notharctus*. The former (with which *Limnotherium* of Professor Marsh is identical) is distinguished by the single roots to the premolars, and by the development of a third lobe to the last lower true molar. *Notharctus* agrees with *Adapis* in the presence of two roots to the premolars, but has a larger lower canine. *Thinolestes* and *Telmatolestes* are probably allied to or identical with the preceding genera; both being from the American Eocene.

Fig. 1349.—Palatal aspect of the left upper cheek-teeth of *Adapis magna*; from the Upper Eocene of Hampshire.

Turning to the more typical representatives of the family, in which at least the upper premolars do not exceed three, we have the small

Necrolemur from the French Phosphorites, the dental formula of which Dr Schlosser gives as $I.\ \frac{2}{1},\ C.\ \frac{1}{1},\ Pm.\ \frac{3}{3},\ M.\ \frac{3}{3}$, or the same as in the existing *Tarsius*, although he suggests that in some cases there may have been four lower premolars. The skull resembles that of the living genus *Galago* of Africa, both in size and structure, as is especially shown by the prominent auditory bullæ. The upper molars are also like those of one species of that genus, although the

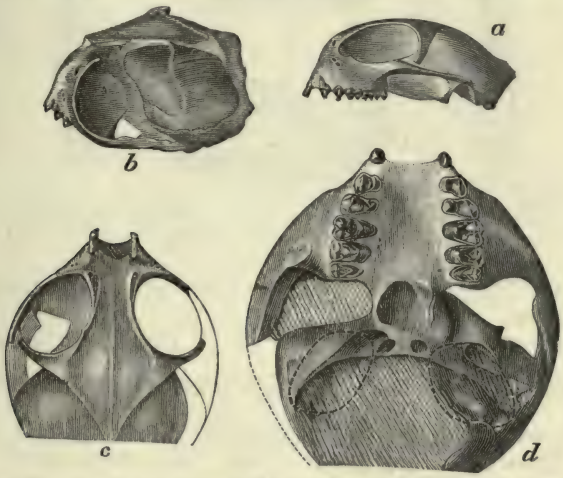


Fig. 1350.—Cranium of *Anaptomorphus homunculus;* from the Wasatch Eocene of North America. *a*, From the left side; *b*, Oblique view; *c*, From above; *d*, From below (enlarged). (After Cope.)

last premolar is distinguished by having only one outer column, and is accordingly simpler than the true molars. In this respect *Necrolemur* agrees with *Chirogaleus* of Madagascar.

Plesiadapis, from the Lower Eocene of Rheims, may be provisionally placed here. *Anaptomorphus*, from the Middle Eocene of North America, of which the cranium and mandible are shown in the accompanying figures, seems to be allied to *Necrolemur*, but has two lower incisors, and the upper premolars are unusually complex and approach those of the *Anthropoidea*. The upper molars are tritubercular; and Professor Cope gives the dental formula as $I.\ \frac{2}{2}$, $C.\ \frac{1}{1}$, $Pm.\ \frac{2}{2}$, $M.\ \frac{3}{3}$. *Cynodontomys* is an imperfectly known genus from the Wasatch Eocene; and *Mixodectes* an older one from the Puerco or Lower Eocene of North America. Dr Schlosser also regards the American Eocene genus *Omomys* as allied to *Necrolemur*,

although it was considered by Professor Cope to be more nearly related to *Hyopsodus*. *Lemuravus*, of the American Eocene, may perhaps belong to the preceding division of this family.

The total absence of remains of Lemuroids from the Miocene of

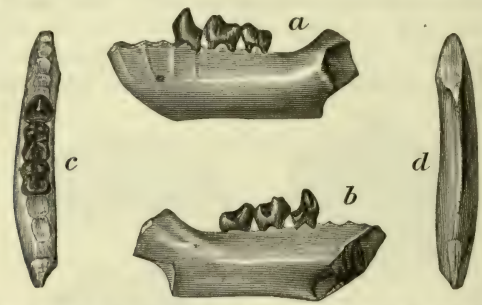


Fig. 1351.—Left ramus of the mandible of *Anaptomorphus æmulus*, wanting all the teeth except the last premolar and first two true molars; from the Bridger Eocene of North America. *a*, Outer; *b*, Inner; *c*, Upper; *d*, Lower view. Twice natural size. (After Cope.)

Europe and North America points to their early disappearance from those regions.

Suborder 2. Anthropoidea.—In all the known members of this suborder the number of the incisors is $\frac{2}{2}$; the upper ones being always in contact in the middle line, and the lower ones not projecting forwards to any great extent. The orbit is completely closed behind by bone; and the lachrymal foramen opens within its cavity. The pollex is short, and the second digit of the pes has a true nail. This suborder may be divided into the *Platyrhine* and *Catarhine* sections. In the former, which is confined at the present day to South America, the structure of the cheek-teeth is intermediate between that obtaining in the Lemuroidea and the succeeding section. The premolars are always $\frac{3}{3}$ in number, but the true molars may be either $\frac{2}{2}$ (*Hapalidæ*), or $\frac{3}{3}$ (*Cebidæ*); and the last lower true molar has a small hind talon. The nostrils are simple, widely separated, and placed nearly at the extremity of the snout. The pollex is either absent, or, if present, is not opposable; and there are other characteristic external features.

The genus *Laopithecus*, from the Miocene of North America, has been referred to this section, but its dentition approximates to that of the early Lemuroids, and its position must be regarded as unsettled.

Family Hapalidæ.—In the Marmosets, which are nearest to the

Lemuroidea, two species of *Hapale* have been recorded from the cave-deposits of Brazil, one of which is regarded as extinct.

Family Cebidæ.—The Brazilian cave-deposits have also yielded remains of various *Cebidæ* referable to the existing genera *Callithrix*, *Cebus*, and *Mycetes;* several of which appear indistinguishable from species still inhabiting the same region. A monkey allied to *Mycetes*, but of larger size than any existing species, has been referred to a distinct genus under the name of *Protopithecus*.

Catarhine Section.—In this section, which comprises the three families *Cercopithecidæ*, *Simiidæ*, and *Hominidæ*, the number of the cheek-teeth is always $Pm. \frac{2}{2}$, $M. \frac{3}{3}$, and the crowns of the true molars are either transversely ridged or simply tubercular. The nostrils are straight, and placed close together, and their septum is narrow. In all except *Colobus*, where it is absent, the pollex is opposable to the other digits. The tail is never prehensile, and may be wanting; while cheek-pouches and ischial callosities are often present. With the exception of one species, which occurs at Gibraltar, all the existing *Cercopithecidæ* and *Simiidæ* are confined to Asia and Africa.

Family Cercopithecidæ.—In this family, which includes most of those Old World genera commonly termed Monkeys and Baboons, the tubercles of the true molars are developed into a pair of imperfect transverse ridges, and the third lower true molar has a hind lobe or talon. It has been stated that the genus *Colobus* occurs in the Miocene of Bavaria, but the specimen on which this determination was made really belongs to the Artiodactylate genus *Cebochœrus*. The somewhat widely spread genus *Macacus* is represented in the Pliocene Siwaliks of India, and also in the Upper Pliocene of the Continent and the Pleistocene of India; one of these continental species having probably been described under the name of *Aulax-*

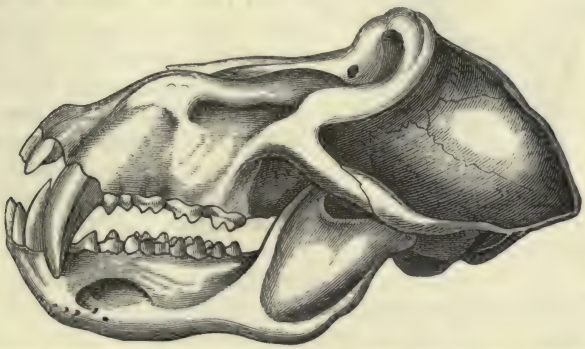


Fig. 1352.—Left lateral view of the skull of *Cynocephalus ursinus;* Recent. Africa. Reduced.

inus. The Asiatic genus *Semnopithecus* is known by remains of existing species in the Indian Pleistocene, and by extinct forms in the Siwaliks of the same country, and also in the Lower Pliocene of France and Italy. *Mesopithecus*, from the Lower Pliocene of Greece and Hungary, is an extinct genus allied in cranial characters to *Semnopithecus*, but in the structure of the limbs approximating to *Macacus*. The genus *Cynocephalus*, now confined to Africa, and characterised by the long and projecting facial region and the nearly vertical position of the orbits (fig. 1352), is found fossil in the Pliocene Siwaliks of India, and in the Pleistocene of Southern India and Algeria; and thus indicates the intimate relations of the Indian and African faunas. *Oreopithecus*, from the Middle Miocene of Italy, was probably allied to the preceding genus, but only an immature mandible is known.

Family Simiidæ.—In the *Simiidæ*, which includes the Gibbons, Orangs, Chimpanzees, and Gorillas, the tubercles of the cheek-teeth (fig. 1353) are low and blunt, and the angles of their crowns are more or less rounded off, and the third lower true molar has no hind talon. The canines are large, and the hallux is opposable. The Gibbons are represented in a fossil state in the Pleistocene of Borneo by a species of *Hylobates*, and by another from the Middle Miocene of France which may be included in the same genus, although separated by some under the name of *Pliopithecus*. *Dryopithecus*, from the Middle Miocene of France and the Lower Miocene of Hessen-Darmstadt, was a large Ape of the size of the Chimpanzee, but with teeth resembling those of the Gorilla. Lastly, the Pliocene Siwaliks of India have yielded a species of *Anthropopithecus* (*Troglodytes*) apparently closely allied to the existing African Chimpanzee; while there are also indications in the same deposits of a species of the Malayan genus *Simia* (Orang). A skull of the existing species of *Simia* is shown in woodcut, fig. 1354.

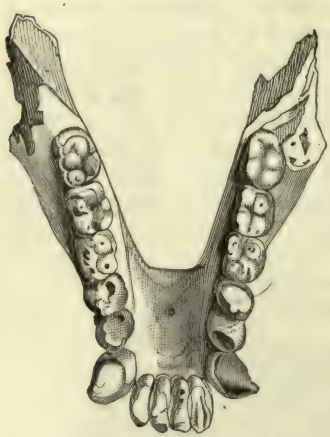


Fig. 1353.—Palatal aspect of the mandible of *Hylobates antiquus*; from the Middle Miocene of France.

Family Hominidæ.—The last and highest family of the class comprises only Man (*Homo*), and requires but little notice in this work. It may, however, be observed that the teeth form a nearly even horse-shoe-shaped series, without any diastema or marked increase in the size of the canine, and are thus in striking contrast

to those of the *Simiidæ* (compare A and B in fig. 1354); although their number and structure are identical. The skull is also remarkable for the great relative size of the cranial, and the shortness of the facial portion.

Man has certainly existed throughout the Pleistocene period, and there is also evidence of his presence at the epoch of the St Prest beds of the south of France, which are equivalent to the Norfolk Forest-bed, and are referred by some authorities to the base of the Pleistocene, and by others to the top of the Pliocene. Somewhat doubtful evidence of his existence in the true Pliocene of Italy has

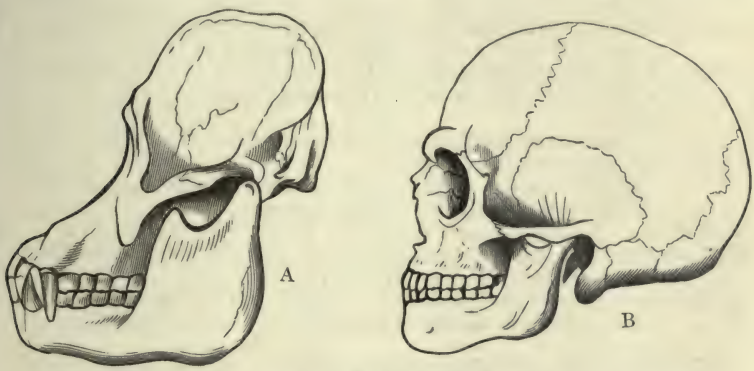


Fig. 1354.—Left lateral view of the skull of (A) the Orang (*Simia*) and (B) a European. Reduced.

been brought forward; and it has been asserted that a skull found in Calaveras county, in the United States, is from Pliocene beds. In the latter instance, however, some authorities doubt whether the skull in question was really obtained from these beds, while others consider that the beds themselves are not earlier than the Pleistocene. Far stronger proofs than those hitherto brought forward must be forthcoming before the alleged existence of Man in the Middle Miocene of France can be accepted. The evidences of his existence in the Recent period belong rather to the domain of the archæologist and ethnologist than to that of the palæontologist.

In conclusion, it may be mentioned that Professor Cope regards the *Hominidæ* as having originated independently of the other Anthropoidea from a Lemuroid stock; but much more conclusive evidence than that yet adduced is necessary to support this view.

LITERATURE OF MAMMALIA.

1. ADAMS (A. LEITH).—"British Fossil Elephants." 'Mon. Pal. Soc.' (1877-78).
2. —— "Dentition and Osteology of the Maltese Fossil Elephants." 'Trans. Zool. Soc.,' 1874.
3. BURMEISTER (H.)—"Description Physique de la Républic Argentine, &c.," vol. iii. Buenos Ayres (1879).
4. —— Various memoirs in the 'Annales del Museo Publico do Buenos Aires,' vols. i.-iii.
5. CAPELLINI (G.)—Numerous memoirs on Fossil Cetacea in Italian Serials.
6. COPE (E. D.)—"Vertebrata of the Tertiary Formations of the West," book i. 'Rep. U.S. Geol. Surv. Terrs.,' vol. iii. (1884).
7. —— "Vertebrate Palæontology of Territory West of 100th Meridian," 'Rep. U.S. Geol. Surv. W. of 100th Meridian,' vol. iv., pt. 2 (1877).
8. —— "Synopsis of the Fauna of the Puerco Series." 'Trans. Amer. Phil. Soc.,' vol. xvi. (1888).
   See also various memoirs in 'American Naturalist,' and 'Proc. of Philadelphia Academy of Nat. Science.'
9. CUVIER (G.)—"Ossemens Fossiles." 2d. ed. Paris (1821-25).
10. DAWKINS (W. B.), and SANFORD (W.)—"British Pleistocene Mammalia." 'Mon. Pal. Soc.' (1866-71).
11. DEPÉRET (C.)—"Recherches sur la Succession des Faunes de Vertèbres Miocènes de la Vallée du Rhone." 'Arch. Mus. Lyon,' vol. iv. (1886).
12. FALCONER (H.)—"Palæontological Memoirs and Notes of." Edited by C. Murchison. London (1868).
13. —— and CAUTLEY (P. T.)—"Fauna Antiqua Sivalensis." London (1846-49).
14. FILHOL (H.)—"Etude des Mammifères Fossiles de St Gérand-le-Puy, Allier." 'Ann. Sci. Géol.,' vols. x. and xi. (1879-81).
15. —— "Etude des Mammifères Fossiles de Ronzon, Haute-Loire." 'Ann. Sci. Géol.,' vol. xii. (1882).
16. —— "Recherches sur les Mammifères Fossiles du Quercy." 'Ann. Sci. Géol.,' vols. vii., viii. (1876-77).
   See also vol. xvii. of the same serial.
17. FLOWER (W. H.)—"Catalogue of Osteological Specimens in the Museum of the Royal College of Surgeons," pt. ii., Mammalia. London (1884).
18. —— "Introduction to the Osteology of the Mammalia." 3d ed. London (1885).
19. —— and DOBSON (G. E.)—"Mammalia." 'Encyclopædia Britannica.' 9th ed.
20. GERVAIS (H.), and AMEGHINO (F.)—"Les Mammifères Fossiles de l'Amerique Méridionale." Paris (1880).
21. —— (P.)—"Zoologie et Paléontologie Françaises." 2d ed. Paris (1859).
22. —— "Zoologie et Paléontologie Générales." Two series. Paris (1867-69).
23. —— and VAN BENEDEN (P. J.)—"Ostéographie des Cétacés, Vivants and Fossiles." Paris (1868-79).

24. GAUDRY (A.)—"Animaux Fossiles et Géologie de l'Attique." Paris (1862-67).
25. —— "Animaux Fossiles du Mont Léberon." Paris (1873).
26. —— "Les Enchainements du Monde Animal dans les temps géologiques: Mammifères tertiaires." Paris (1878).
27. HUXLEY (T. H.)—"Manual of the Anatomy of Vertebrated Animals." 2d ed. London (1872).
28. KOWALEVSKY (W.) — "Osteology of the *Hyopotamidæ*." 'Phil. Trans.' (1873).
29. —— "Sur l'*Anchitherium aurelianense*, et sur l'Histoire Paléontologique des Chevaux." 'Mém. Ac. Imp. St Pétersburg,' vol. xx. (1873).
30. LEIDY (J.)—"The Extinct Mammalian Fauna of Dakota and Nebraska." 'Journ. Ac. Nat. Sci. Philadphia.,' vol. vii. (1869).
31. —— "The Extinct Vertebrate Fauna of the Western Territories." 'Rep. U.S. Geol. Surv. Terrs.,' vol. i. (1873).
32. LÉMOINE (V.)—"Etude sur quelques Mammifères de petite taille de la Faune Cernaysienne des environs de Reims." 'Bull. Soc. Géol. France,' vol. xii. (1885).
33. —— Earlier memoirs on this subject in the same serial.
34. LYDEKKER (R.)—"Catalogue of the Fossil Mammalia in the British Museum," pts. i.-v. London (1885-87).
35. —— "Fossil Vertebrata of India." 'Rec. Geol. Surv. Ind.,' vol. xx. (1887).
36. —— "Indian Tertiary and Pretertiary Vertebrata." 'Palæontologia Indica—Mem. Geol. Surv. Ind.,' ser. 10, vols. i.-iv. (1875-86).
37. MAJOR (C. J. FORSYTH).—"Beiträge zur Geschicte der Fossilen Pferde, inbesondere Italiens." 'Abh. Schweiz. pal. Ges.', vols. iv.-vii. (1877-80).
38. MARSH (O. C.)—"Dinocerata, a Monograph of an Extinct Order of Gigantic Mammals." 'Rep. U.S. Geol. Surv.,' vol. x. (1884).
39. —— Various memoirs in the 'American Journal of Science' and other American serials.
40. —— "American Jurassic Mammals." 'Geol. Mag.,' 1887, pp. 241, 289.
41. MIVART (ST G.)—"On the Possibly Dual Origin of the Mammalia." 'Proc. Royal Soc.,' vol. xliii., p. 372 (1888).
42. OSBORN (H. F.)—"The Structure and Affinities of the Mesozoic Mammalia." 'Journ. Acad. Nat. Sci. Philadelphia,' vol. ix., pt. 2 (1888). "Additional Observations on the same." 'Proc. Ac. Nat. Sci. Philad.,' Oct. 1888.
43. OWEN (R.)—"Extinct Fossil Mammalia of Australia." London (1877).
44. —— "Fossil Mammalia of the British Mesozoic Formations." 'Mon. Pal. Soc.' (1871).
45. —— "History of British Fossil Mammals and Birds." London (1846).
46. —— "Odontography." London (1840-45).
47. —— "Memoir on the *Mylodon*." London (1842).
48. —— "Memoir on the *Megatherium*." London (1860).
49. —— Various memoirs in the serials of English scientific societies.
50. —— "Zoology of the Voyage of the Beagle — Fossil Mammalia." London (1840).
51. PARKER (W. K.)—"On Mammalian Descent." London (1885).
52. POULTON (E. B.)—"The True Teeth and the Horny Plates of *Orni-*

thorhynchus." 'Quart. Journ. Microscopical Science,' 1888, p. 9.

53. ROGER (O.)—"Verzeichniss der bisher bekannten fossilen Saügethiere." 'Verhandl. Mittheil. nat. Vereins Augsburg,' 1887.
54. RÜTIMEYER (L.)—"Beiträge zu einer Natürlichen Geschicte der Hirsche." 'Abh. Schweiz. pal. Ges.,' vols. vii.-x. (1880-83).
55. —— "Die Rinder der Tertiär-Epoche, &c." 'Abh. Schweiz. pal. Ges.,' vols. iv., v. (1877-78).
56. —— "Eocäne Saügethiere aus dem Gebiet des Schweizerischen Jura." 'Denschr. Schweiz. Ges. Nat.,' vol. xix. (1862).
57. —— "Weitere Beiträge zur Beurtheilung der Pferde der Quaternär-Epoche." 'Abh. Schweiz. pal. Ges.,' vol. ii. (1875).
58. SCHLOSSER (M.)—"Beiträge zur Kenntniss der Stammesgeschicte der Hufthiere, &c." 'Morphol. Jahrbuch,' vol. xii. (1886).
59. —— "Die Nager des Europäischen Tertiärs." 'Palæontographica,' vol. xxi. (1884).
60. —— "Die Affen, Lemuren, Chiropteren, Insectivoren, Creodonten, und Carnivoren des Europäischen Tertiars." 'Beiträg. z. Paléontologie Oesterr-Ungar.,' vols. vi., vii. (1887-88).
61. SCOTT (W. B.)—"On some New and Little-known Creodonts." 'Journ. Ac. Nat. Sci. Philad.,' vol. ix. (1887).
62. —— "Notes on the Osteology and Systematic Position of *Dinictis felina*, Leidy." 'Proceedings American Phil. Soc.' (1889).
63. TELLER (F.)—"Neue Anthracotherienreste aus Süd-Steiermärk und Dalmatien." 'Beiträg. z. Paléontologie Oesterr-Ungar.,' vol. iv. (1884).
64. THOMAS (O.)—"On the Dentition of *Ornithorhynchus*." 'Proceedings Royal Society,' 1889.
65. VACEK (M.)—"Ueber Österreichischen Mastodonten, &c." 'Abh. k. k. geol. Reichs.,' vol. vii. (1877).
66. VAN BENEDEN (P. J.)—Various memoirs on the Fossil Cetacea of Belgium, published in the 'Bull. Ac. R. Belgique' and the 'Ann. Mus. R. Hist. Nat. Belgique.'
67. WEITHOFER (K. A.)—"Beiträge zur Kenntniss der Fauna von Pikermi, bei Athen." 'Beiträg. z. Paléontologie Oesterr-Ungar.,' vol. v. (1888).
68. —— "Die fossilen Hyänen des Arno-thaler in Toskana." 'Denkschr. k. Akad. Wien.,' vol. lv. (1889).

It should be mentioned that neither the above nor the preceding lists of memoirs make any approach to a complete bibliography of their respective subjects. They are merely intended to indicate to the student the sources where he will most readily obtain information, and in many cases important memoirs of an early date are not mentioned, since they are quoted in those given in the lists.

PART IV.

PALÆOBOTANY

BY

H. ALLEYNE NICHOLSON AND R. LYDEKKER

PART IV.

CHAPTER LXIV.

CLASSIFICATION AND GENERAL SUCCESSION OF PLANTS IN TIME.

The department of Palæontology which deals with the relations of Plants to time is usually spoken of under the name of Palæobotany or Palæophytology, and is one of wide extent and great complexity. To render adequate justice to the vast body of knowledge which has been accumulated as to the past history of plants, an amount of space much exceeding that available in the present work would be required. Moreover, the subject is one which cannot be thoroughly dealt with except by a specialist, and which, in itself, is of less importance to the general geological student than is Palæozoology. For these reasons, nothing more will be attempted here than to give an extremely brief and entirely general sketch of the past distribution and succession of the chief types of plant-life; the extinct groups being treated with somewhat greater detail than those now in existence. In most cases, however, no description of the characteristic structures of the different groups can be given; nor is it possible to introduce so much as a sketch of the general morphology of plants. For such the student must be referred to works devoted to structural Botany, to which he must also look for the meaning of such technical terms as are here made use of.

CLASSIFICATION.

As regards the classification of Plants, the following table shows the leading groups into which the existing members of the Vegetable Kingdom are divided :—

KINGDOM VEGETABILIA.

SUB-KINGDOM A.—THALLOPHYTA.

SERIES I.—ALGÆ.

Class 1. Diatomaceæ . . .	Diatoms.
,, 2. Phycochromophycæ .	Desmids.
,, 3. Fucaceæ	Sea-weeds.
,, 4. Chlorosporeæ . .	*Siphoneæ.*
,, 5. Florideæ . . .	Red Sea-weeds, Corallines, and Nullipores.
,, 6. Characeæ . . .	Charas.

SERIES II.—FUNGI.

This series includes the Lichens (*Lichenes*) and the true Fungi, the latter being split into several divisions which need not be inserted here.

"Cryptogams," or Non-Flowering Plants.

SUB-KINGDOM B.—CORMOPHYTA.

SERIES I.—BRYOPHYTA (Anogens).

Class 1. Musci	Mosses.
,, 2. Hepaticæ . . .	Liverworts.

SERIES II.—PTERIDOPHYTA (Acrogens).

Class 1. Filicaceæ.	
Order 1. Stipulatæ.	
a. Ophioglosseæ . . .	Adders'-tongues.
b. Marattiaceæ . . .	Marattia.
Order 2. Filices . . .	Ferns.
Order 3. Rhizocarpeæ . .	Rhizocarps.
Class 2. Equisetaceæ . . .	Horsetails.
Class 3. Lycopodiaceæ.	
Order 1. Isosporeæ (*Dichotomæ*).	
a. Lycopodeæ . . .	Lycopods.
b. Psiloteæ . . .	
c. Phylloglosseæ . . .	
Order 2. Heterosporeæ (*Ligulatæ*).	
a. Selaginelleæ . . .	Club-mosses.
b. Isoëteæ	

"Phanerogams," or Flowering Plants.

SERIES III.—PHANEROGAMÆ.

Class 1. Gymnospermeæ.	
Order 1. Cycadaceæ . .	Cycads.
Order 2. Coniferæ . .	Conifers.
Order 3. Gnétaceæ . .	Welwitschia.
Class 2. Angiospermeæ.	
Subclass 1. Monocotylæ (Endogens) . . .	Grasses, Palms, Lilies, &c.
,, 2. Dicotylæ (Exogens)	Rose, Buttercup, Dandelion, &c.

The above classification is, in the main, the one adopted by Professor Thistleton Dyer, although a less complex arrangement of the

Thallophytes has been adopted. The divisions of the Fungi, as being of no importance to palæontologists in the present state of our knowledge, have likewise been omitted; as, also, have been several of the groups of the Algæ. In older botanical systems, plants, in place of being ranged into the two primary divisions of Thallophytes and Cormophytes, were separated into "Cryptogams" and "Phanerogams," the limits of these old divisions being indicated in the margin of the above table; and it will still be sometimes convenient to employ the former term as a collective name for the non-flowering plants. Similarly, the Cryptogams were formerly divided into Thallogens, Anogens, and Acrogens; and we still very generally meet with the two latter terms (the position of which is indicated in brackets in the table) in geological works, where the expression "Age of Acrogens" has become almost classical. It is, however, very inadvisable to retain for geological purposes a classification abandoned by the more advanced botanists; and we shall therefore adopt the names Bryophytes and Pteridophytes in place of the older Anogens and Acrogens.

The Thallophytes are cellular plants not distinctly differentiated into stem and leaf; the *Algæ* being distinguished from the *Fungi* by the presence of chlorophyll. The Bryophytes, while still wholly cellular, may have distinct stems and leaves; while the Pteridophytes are partly composed of cells and partly of long tubes or vessels, and are thus fitted for the attainment of considerable dimensions. The Phanerogams are like the Pteridophytes in being vascular plants, but differ from all the preceding groups in developing flowers, which in turn produce seeds containing an embryo. The series of the Phanerogams is again divided into the Gymnosperms, with naked seeds not enclosed in fruits, and the Angiosperms, in which true fruits enclose the seeds. This latter group is further divisible into two sections, known, from the number of the seed-leaves, as Monocotyledons and Dicotyledons. In the Monocotyledons the embryo has only a single seed-leaf or cotyledon, and the stems grow from within and show no rings of growth; the name of "Endogens" applied to the group being based on this latter feature. In the Dicotyledons, on the other hand, the embryo has two seed-leaves or cotyledons; and the group is sometimes spoken of as that of the "Exogens," since the stems (as in the Gymnosperms also) grow from without, with the formation of distinct rings of growth.

General Succession of Plants in Time.

As in the Animal Kingdom, so among plants there appears to be a general correspondence between relative rank in the scale of organisation and the order of appearance in time. Thus, as Sir William

Dawson observes, "the oldest plants that we as yet certainly know are Algæ, and with these there are plants apparently with the structure of Thallophytes, but the habits of trees, which for want of a better name I may call Protogens" [Nematodendreæ]. "Plants akin to the Rhizocarps also appear very early. Next in order we find forests in which gigantic Ferns, Lycopods, and Horsetails predominate, in association with Pines. Succeeding these we have a reign of Gymnosperms; and in later formations we find the higher Phanerogams dominant. Thus there is an advance in elevation and complexity along with the advance in geological time, but connected with the remarkable fact that in earlier periods low groups attain to an elevation unexampled in later epochs, when their places are occupied with plants of higher types."[1]

The age of Algæ and Nematophytes corresponds with the earlier portion of the Palæozoic period, while Pteridophytes, with some Gymnosperms, are the dominant forms of the later Palæozoic deposits. The Mesozoic period may be termed the "Age of Gymnosperms," while the Angiosperms assume the leading place in the Tertiary. The floras of the great geological periods, however, shade gradually into one another, and no hard-and-fast lines can be drawn between them. Thus, we have already seen that Gymnosperms make their first appearance in the Upper Palæozoic rocks, these ancient types being the precursors of the characteristically Gymnospermous flora of the Mesozoic period. In a similar manner the Upper Cretaceous flora, by its great development of Angiosperms, is more nearly related to the Tertiary than to the preceding Jurassic flora. Moreover, the evolution of the flora of different regions of the earth by no means advanced *pari passu* with the evolution of the fauna—a striking example of this fact being afforded by the Lower Gondwana beds of India and the equivalent deposits of Australia, in which, reckoning from a European standpoint, we find a full-blown Mesozoic flora coexisting with a Palæozoic fauna.

Taking a brief historical retrospect of the distribution of plants in time, we have no direct evidence of the existence of vegetable life during the period represented by the Archæan rocks. There is, however, a strong probability in favour of Sir William Dawson's view that the extensive accumulations of graphite associated with the Laurentian limestones of Canada are really of the nature of metamorphosed vegetable matter, or that they have been derived in the first instance from plants. In deposits of Cambrian age most of the supposed remains of plants belong to the obscure and difficult group of fossils commonly spoken of as "Fucoids," and supposed to be referable to the Sea-weeds. So far as the "Fucoids"

[1] Some slight verbal alterations have been made in this quotation.

of the Cambrian rocks are concerned, there is every probability that we have to deal entirely with the tracks and trails of marine animals, or with impressions of a purely inorganic character. Thus, the Cambrian fossils referred to such genera as *Cruziana* and *Bilobites* are most probably the tracks of Annelides, or the filled-up burrows of Crustaceans. The fossils from the Cambrian rocks of Sweden described under the name of *Eophyton*, and at one time supposed to be the remains of land-plants, are almost certainly not of a vegetable nature. As previously pointed out (p. 209), strong evidence has been brought forward by Nathorst in favour of the view that the striated markings of *Eophyton* are really produced by the trailing of the tentacles of Jelly-fishes over the surface of soft sediment. Lastly, the so-called *Oldhamia* of the Cambrian rocks (p. 205) has been regarded as an Alga, but it may have been produced by animal agency, or it may be wholly inorganic.

From strata of Ordovician age many supposed plants have been

Fig. 1355.—*Licrophycus Ottawaensis*, a supposed "Fucoid" from the Trenton Limestone (Ordovician) of Canada. (After Billings.)

described, and the great majority of these have been referred to the *Algæ*, and have been regarded as the remains of Sea-weeds. Most

of these so-called "Fucoids" are wholly destitute of carbon, and are almost certainly not of a vegetable nature. Many of these supposed Sea-weeds—such as those referred to the genera *Palæochorda* and *Crossopodia* (the *Crossochorda* of Schimper)—present themselves as simple, often sinuous or convoluted, raised markings on the surface of muddy or arenaceous sediments. Such markings, as specially insisted on by Nathorst, always occur in demi-relief on the *under* surfaces of the beds in which they are found; and this fact would strongly support the view that they are really the *casts* of the trails of marine animals such as Worms or Molluscs, such trails presenting themselves as depressed impressions on the *upper* surfaces of the strata. Raised impressions on the under sides of the strata, but branched, are not uncommon, and upon these have been founded such genera as *Licrophycus* (fig. 1355). These curious fossils may be regarded as probably of the nature of filled-up worm-burrows, rather than as mere surface-trails.

On the other hand, some of the so-called "Fucoids" of the Ordovician, as also of the Silurian rocks, appear to be truly the

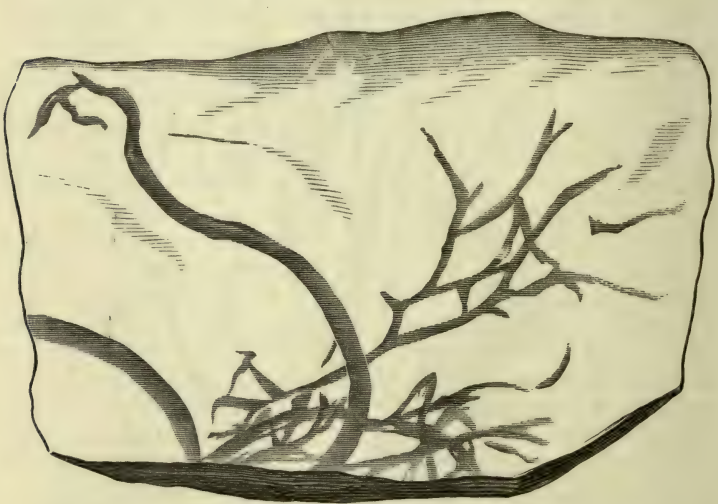


Fig. 1356.—*Buthotrephis gracilis*, Hall; a "Fucoid" from the Trenton Limestone (Ordovician) of Ottawa. (Original.)

remains of marine *Algæ*. This is the case, for example, with some of the fossils which have been referred to the genus *Buthotrephis* of Hall. The types in question (fig. 1356) present themselves as compressed, branching impressions, sometimes showing leaf-like extremities, and occasionally distinctly carbonaceous.

In addition to *Algæ*, the Ordovician rocks have yielded a few unquestionable plant-remains which are regarded by Dawson as probably having been of a higher grade. Thus, the *Protannularia* of the Arenig rocks of Britain, and the *Sphenothallus* of the Cincinnati group of North America, are provisionally referred to the Rhizocarps; while the *Protostigma* of the latter formation is looked upon as possibly allied to the Lycopods.

In the Silurian rocks we meet with various Sea-weeds of an apparently unquestionable character, and along with these are found the remains of plants of a higher type. The most abundant of these belong to the genus *Psilophyton*, regarded by Dawson as forming a connecting link between the Rhizocarps and the Lycopods. The *Glyptodendron* of the Clinton beds may perhaps be related to *Lepidodendron*, but the supposed Silurian fern, described under the name of *Eopteris*, is not truly organic. Lastly, in the Silurian rocks are found the first traces of the singular tree-like plants originally described by Dawson under the name of *Prototaxites*, but now termed *Nematophyton*. The characters of this will be briefly noted immediately; but it may be mentioned here that the curious spore-like bodies, which have been described from the Silurian rocks under the name of *Pachytheca*, are regarded by Dawson as not improbably belonging to this plant.

In the Devonian rocks, as more especially shown by Sir William Dawson, we have evidence of an abundant flora, consisting of both aquatic and terrestrial plants. Of the Devonian fossils which have been referred to the *Algæ*, the most singular is the genus *Spirophyton*, comprising certain broad, spirally twisted impressions, which are very abundant in some of the lower beds of the Devonian series of North America. Similar impressions—often spoken of under the name of "Cauda Galli"—occur in the Lower Carboniferous rocks of Europe; but their real nature is not free from doubt. We may also notice here the highly remarkable tree-like plants for which the genus *Nematophyton* (*Prototaxites*) has been proposed by Dawson, since these cannot at present be definitely referred to any recognised group of existing plants. According to Dawson, the plants in question (fig. 1357) are "trees of large size, with a coaly bark and large spreading roots, having the surface of the stem smooth or irregularly ribbed, but with a nodose or jointed appearance. Internally, they show a tissue of long, cylindrical tubes, traversed by a complex network of horizontal tubes, thinner-walled and of smaller size." The tubes appear to be arranged in concentric zones, but the plant was not truly exogenous, and it is doubtful if a genuine bark was present. The systematic place of *Nematophyton* is uncertain, but the balance of evidence would seem to be in favour of its reference to the Thallophytes, and it is regarded by Dawson as

the type of a special group, for which he has proposed the name of *Nematodendreæ*. The same authority is of opinion that the minute globular bodies to which the name of *Pachytheca* has been given,

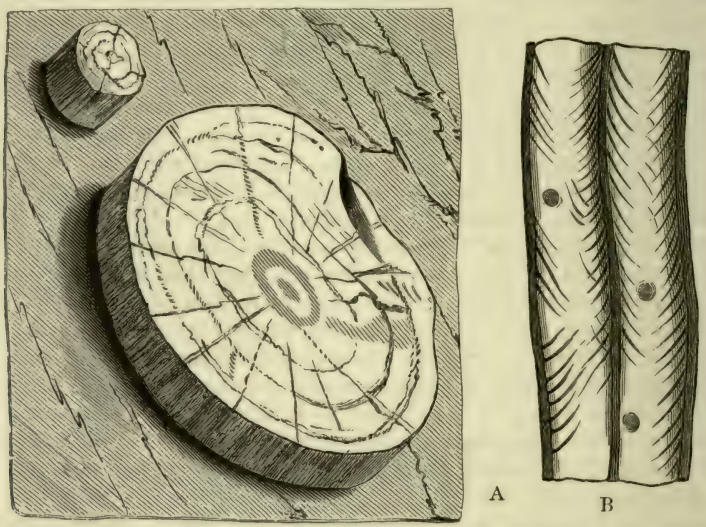


Fig. 1357.—A, Trunk of *Nematophyton* (*Prototaxites*) *Logani*, 18 inches in diameter, as seen in the cliff near L'Anse Brehaut, Gaspé; B, Two of the tubular cells forming the tissue of the stem, highly magnified. Lower Devonian, Canada. (After Dawson.)

may perhaps have been the fruit of *Nematophyton*. As previously noted, the genus occurs also in the Silurian rocks.

Coming to higher plants, the Rhizocarps are represented in the Devonian flora by such types as *Sphenophyllum* and *Psilophyton*, the latter showing affinities with the Lycopods. Moreover, some of the Devonian shales of North America are crowded with minute globular thick-walled bodies (fig. 1358), of a diameter of one-hundredth of an inch or more, which Dawson regards as being probably of the nature of the "macrospores" of plants allied to the Rhizocarps. These were originally described under the name of *Sporangites Huronensis*, but they are now referred by Dawson to the provisional genus *Protosalvinia*. Similar bodies have been shown to occur, often in vast numbers, in shales of Carboniferous age in both North America and Europe, and even some coals appear to be largely made up of structures of a similar nature.

Of still higher groups of plants, the Devonian rocks have yielded the remains of *Lepidodendron* and *Sigillaria*, representing the Lycopods, and of early types of Calamites, representing the Horsetails; while true Ferns, some of which attain considerable dimensions, are

present in comparative abundance. Lastly, the Gymnosperms are represented by the woody trunks of Conifers (*Dadoxylon*).

The Carboniferous deposits are remarkable for the richness of their contained flora, as also for the extensive development of beds of workable coal. The predominant plants of this period belong to the groups of the Pteridophytes and Gymnosperms. The former are represented by types belonging to the Rhizocarps, the Ferns, the Lycopods, and the *Equisetaceæ;* though in many cases the Carboniferous plants referred to these groups exhibit quite peculiar characters, and their precise affinities are not always clear. The Rhizocarps are represented by the ancient genus *Sphenophyllum* and by the macrospores of *Protosalvinia*. The latter sometimes occur in vast numbers in the shales of the Carboniferous period, and occasionally play an important part in the formation of coal, though this must be regarded as exceptional. The *Lycopodiaceæ* are represented by the genus *Lycopodites*, but the most remarkable members of this series in Carboniferous times are the tree-like Lepidodendroids (*Lepidodendron*, &c.) The great group of the Sigillarioids (*Sigillaria*, &c.), likewise comprising comparatively gigantic plants, is also usually regarded as belonging to the series of the Lycopods, and is highly characteristic of the Carboniferous deposits. The *Equisetaceæ*, again, are largely represented in Carboniferous times by the remarkable and widely distributed group of the Calamites. Lastly, the Carboniferous rocks have yielded the remains of a large number of true Ferns, which, in most essential respects, are similar to the existing types of the group.

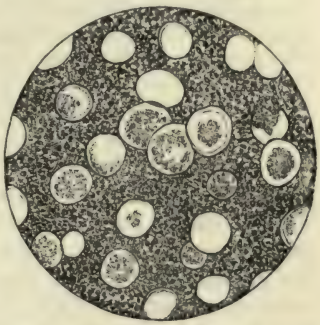


Fig. 1358.—A slice of shale from the Devonian rocks of Kettle Point, Lake Huron, showing the "macrospores" of *Protosalvinia*, magnified. (Original.)

No unquestionable Angiosperms have hitherto been detected in rocks of Carboniferous age, but the Gymnosperms are represented by various Conifers (*Dadoxylon*, *Araucarioxylon*, and *Pinites*).

It is universally admitted that coal is fossilised vegetable matter, and also that, in general, the vegetation which formed the coal grew where the coal-seam is now found. The problem of the precise mode in which the coal-seams of the Coal-measures were formed is largely a geological one, and need not be discussed here. It is sufficient to say here that coal is the result of the bituminisation of vegetable tissues of different kinds, different coal-seams, or different portions of a single seam, being often unlike in their precise structure or mode of formation. According to the researches of Sir William Dawson, the microscopic examination

of coal by means of thin sections shows that the "mineral charcoal" of an ordinary bituminous coal is woody tissue and fibres of bark. The coarser and more laminated portions of the coal are made up of "a confused mass of fragments of vegetable matter belonging to various descriptions of plants." The shining and brilliant layers of coal represent the bark of Sigillarioids or Lepidodendroids preserved in a flattened condition. Certain coals, or parts of certain coals may, further, be extensively composed of the macrospores or microspores of various Carboniferous Cryptogams; but it does not appear that coals are generally made up of such spores for any considerable portion of their mass. Lastly, the microscopical structure and chemical composition of the "cannel-coals," would show that these are "of the nature of the fine vegetable mud which accumulates in the ponds and shallow lakes of modern swamps."

The flora of the Permian period is, on the whole, nearly related to that of the Carboniferous. The Sigillarioids appear now to have become extinct, but the Lepidodendroids seem to have survived into the earlier portion of the Permian period, while the Calamites are represented by the genus *Arthropitys*, and die out at this stage. No undoubted Permian Angiosperms are known, but Conifers are tolerably abundant. Of the latter the genus *Voltzia*, which survives into the Trias, is an old type of the *Taxodineæ;* while *Walchia* connects the Yews with the Araucarias; and the genus *Ullmania* is of interest as producing true cones.

As regards the Mesozoic period, the predominant forms of plant-life in the Triassic, Jurassic, and Lower Cretaceous rocks are Cycads and Conifers; and the name of "Age of Cycads" has sometimes been given to the Mesozoic period, as regarded from a botanical point of view. Ferns, however, occur abundantly in the earlier Mesozoic deposits (Triassic and Jurassic rocks), and true *Equisetæ* make their appearance in the Upper Trias. The first unquestionable remains of Monocotyledonous Angiosperms present themselves in the Mesozoic period, the *Podocarya* and *Kaidacarpum* of the Jurassic rocks appearing to be referable to the Screw-pines (*Pandanaceæ*). True Palms do not appear till the Middle Cretaceous period is reached, but a few remains of Dicotyledonous Angiosperms have been detected in the Lower Cretaceous deposits of Greenland.

While the Lower Cretaceous rocks must be associated botanically with the Jurassic and Triassic, the Upper Cretaceous deposits, on the other hand, are characterised by a flora similar to that of the Tertiary period. From the point of view of the palæobotanist, therefore, the line of division between the Mesozoic and Kainozoic epochs falls to be drawn in the middle of the Cretaceous system. With the coming in of the Upper Cretaceous period, in both the Old and New Worlds, a remarkable change takes place in the characters of the plant-life of the land, the Cycads now assuming a position of comparative insignificance, while the Dicotyledonous Angiosperms undergo a great development and become the dominant forms.

Not only are the ordinary Exogens now the leading forms of plant-life, but many of the Upper Cretaceous types belong to genera now existing. We may therefore regard the Upper Cretaceous period as marking "the advent of the modern flora of the temperate regions of the earth" (Dawson). It follows that the Tertiary floras, regarded generally, more or less closely resemble those now in existence, this resemblance being especially shown in the fact that the predominant forms of plant-life are now the Angiosperms, and, more particularly, the Dicotyledons.

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CHAPTER LXV.

ALGÆ AND FUNGI.

THE plants included in the great series of the *Thallophyta* are separable into the two primary divisions of the *Algæ* and *Fungi*, and are characterised by the fact that they are composed of cells, without true vascular tissue. They may be either unicellular or multicellular, the organism in the latter case forming an expansion or "thallus" which is not differentiated into stem, leaf, and root. In the lower Thallophytes reproduction may be wholly non-sexual; but in the higher forms sexual reproduction takes place, the result being the formation of a spore, or a group of spores, or a fructification within which spores are produced.

SERIES I. ALGÆ.—The group of the *Algæ* includes unicellular or multicellular Thallophytes in which chlorophyll is developed in larger or smaller quantity. They vary extremely in form, and are for the most part inhabitants of water, both fresh and salt. The *Algæ* may be divided into the following six classes, viz. :—

Class I.	Diatomaceæ . . .	Diatoms.
„ II.	Phycochromophycæ .	Desmids.
„ III.	Fucaceæ . . .	Brown Sea-weeds.
„ IV.	Chlorosporeæ . .	*Cymopolia*, &c.
„ V.	Florideæ . . .	Red Sea-weeds, Nullipores.
„ VI.	Characeæ . . .	*Chara* and *Nitella*.

As regards the general distribution of the *Algæ* in time, many forms are quite incapable of preservation as fossils, while others can only be preserved under specially favourable circumstances. In certain groups, however, the organism may secrete a siliceous envelope, or its tissues may undergo calcification, while others become encrusted with carbonate of lime. Such forms readily admit of petrifaction, and unquestionable remains of these occur in the fossil state. Apart from these undoubted fossil *Algæ*, numerous markings

and impressions in rocks of all ages, and especially in the older strata of the earth's crust, have been regarded by palæontologists as the remains of Sea-weeds. The characters and probable mode of origin of many of these so-called "Fucoids" have been already discussed in a general way (see p. 483 and pp. 1481, 1482). It is sufficient to say here that many of the fossils in question may be safely regarded as not belonging to the vegetable kingdom, but as being rather of the nature of the tracks and trails of Worms or Molluscs, or the burrows of Annelides or Crustaceans; while others are of purely inorganic origin. Some "Fucoids," on the other hand, such, for example, as some of the Tertiary or Secondary fossils referred to *Chondrites*, may really be the remains of Sea-weeds. Even, however, in cases where there is a reasonable probability that these so-called "Fucoids" are really Sea-weeds, it is nevertheless impossible to determine definitely to what group of the *Algæ* they belong, since the fructification of the plant is not known. In the following brief account, therefore, of the past history of the *Algæ*, only those groups will be treated of which are of palæontological importance.

Class I. Diatomaceæ.—The Diatoms are unicellular *Algæ*, in which the cell-wall is hardened by the deposition of silica so as to give rise to a glassy case or "frustule," composed of two halves which fit into one another, and which are often minutely sculptured with lines or dots (fig. 1359). The cells may be solitary, or they

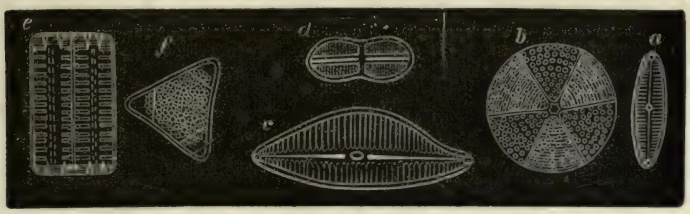


Fig. 1359.—Types of Diatoms, greatly magnified. *a*, *Navicula*, from the Kieselguhr of Franzenbad; *b*, *Actinoptychus*, from Richmond, Virginia; *c*, *Pinnularia*, from Santafiora, Italy; *d*, *Achnanthes*, from Degernfors, Sweden; *e*, *Diatoma*, recent; *f*, *Triceratium*, from the guano of Saldanha Bay, Africa.

may be organically united in rows. Reproduction takes place by the longitudinal fission of the cell, each of the daughter-cells carrying off half of the original cell-wall, and producing the missing half afresh, the two halves of the siliceous case being thus of different ages.

The existing forms of the Diatoms are exceedingly numerous, and have an extraordinarily wide distribution. A few live in moist situations, but the majority are truly aquatic, inhabiting fresh, brackish, or salt waters, peculiar types usually being confined to a special habitat. By the accumulation of their flinty envelopes the Diatoms

give rise, both in the sea and in fresh waters, to very extensive deposits, the general nature of which is that of a fine siliceous mud, sometimes arranged in thin laminæ. Of this nature are the deposits known as "Kieselguhr," "Bergmehl," "Tripoli," and "Polirschiefer," or, simply, as "Diatomaceous Earths." Such deposits may cover wide areas, and may attain a very considerable thickness; and, under an erroneous idea as to their true nature, they have been sometimes spoken of as "Infusorial Earths."

As regards their distribution in time, the cases of Diatoms have been stated to occur in the ashes of the coal of the Coal-measures, but this observation has not been supported by subsequent investigations. In the Middle and Upper Trias whole strata are sometimes largely made up of elongated, parallel-sided, siliceous tubes, with flattened sides and rounded ends, which have been described under the generic name of *Bactrynium*, and which may possibly be Diatoms. If this be their real nature, they are comparatively gigantic members of the class, as they attain a length of from two to four millimetres. Leaving these problematical fossils out of sight, undoubted Diatoms occur in the Upper Chalk, though only a few forms are known. The regular "Diatomaceous Earths" are all of Tertiary or Post-Tertiary age; and among the best known deposits of this epoch may be mentioned the numerous beds of "Kieselguhr" which occupy the sites of ancient lakes in various regions in the northern hemisphere, the "Richmond Earth" of Virginia, the "Tripoli" of Oran in Africa, and Bilin in Bohemia, and the laminated "Polir-schiefer" of Cassel.

Class II. Phycochromophycæ.—The *Algæ* included in this class are unicellular or multicellular, usually bluish-green in colour, and inhabit water or live in moist places on land. Reproduction takes place by cell-division, or by the formation of asexually-produced cells ("gonidia"). The integument is not hardened by the deposition of silica within it. In this class are included numerous widely distributed forms of the *Algæ*, such as the *Oscillariæ*, the Nostocs, and the Desmids. Owing to the soft nature of their outer covering, no undoubted remains of this class of *Algæ* have been detected in the fossil condition; but remains of *Nostoc* are said to occur in strata of Tertiary age, and the curious spherical and spined bodies which are known as *Xanthidia*, and which are sometimes recognisable under the microscope in thin sections of flint or chert, have been supposed to be the spores of Desmids.

Class III. Fucaceæ.—This class includes the common brown Sea-weeds, and comprises forms which are often of considerable size and of various shape. The thallus is often foliaceous and much branched, or may be more or less filamentous. The reproductive organs are developed in special cavities or "conceptacles." The

integument is not hardened by the deposition of lime or flint. Certain Tertiary fossils have been described by palæobotanists as belonging to this group of Sea-weeds, but the nature of many of these is very doubtful.

Class IV. Chlorosporeæ.—This class includes a number of green or olive-coloured Algæ, which live in the sea or in fresh waters, and which reproduce themselves by cell-division or by the development of spores in special cavities, while swarm-spores occasionally exist. The only group of this class which attains sufficient palæontological importance to require special notice is that of the *Siphoneæ verticillatæ*. This family includes green-coloured marine Algæ, in which the thallus consists of a single cell, which may or may not be hardened by the deposition of carbonate of lime in its wall. The single cell which constitutes the entire plant may be of gigantic size, comparatively speaking, and may be simple or branched. At its base the cell sends out root-like prolongations, by means of which it is attached to foreign bodies; while its ascending portion gives origin to whorls of lateral tubular processes. Reproduction takes place by the development of swarm-spores in special cavities or chambers. The few living forms of this family (*Cymopolia*, *Neomeris*, *Acetabularia*, &c.) are inhabitants of warm seas; and with these must be associated an extensive series of fossil types, which have been commonly regarded as referable to the *Foraminifera* or the Corals, and the real nature of which was first demonstrated by Munier-Chalmas.

As above pointed out, the thallus of the *Siphoneæ verticillatæ* may be simple or dichotomously branched, and consists of a single axial cell, which is fixed to foreign bodies by root-like basal extensions. The unicellular, often divided, axis gives out at intervals whorls of short tubular processes (fig. 1360, B), the point of origin of each whorl being commonly marked by a constriction of the stem. In some cases (*e.g.*, in *Ovulites* and *Diplopora*) the primary whorled processes do not subdivide; but in others (*e.g.*, in *Cymopolia*) the primary offshoots (fig. 1360, C, *c*) divide again into secondary processes, some of which (*b*) are sterile, while others (*a*) are connected with reproduction. The sterile offshoots terminate in free extremities which are often dilated and club-shaped, and by their apposition give rise to a porous superficial layer. The fertile offshoots, on the other hand, constitute spherical sporangia (*a*), which are wider than the sterile processes, and are at the same time supported upon shorter stalks.

In many forms, both the axis and the verticillate processes derived from it secrete a thick calcareous crust. Where the lateral whorled offshoots are simple (as in *Diplopora*), the calcareous crust has the form of a simple thickened cylinder, traversed by transverse tubes,

which correspond with the lateral processes, and open by pores upon the surface. On the other hand, where there are two orders of lateral offshoots (as in *Cymopolia*), a double calcareous cylinder is produced, the inner one corresponding with the axis and the primary whorled processes, while the outer one is formed by the confluent clavate ends of the secondary processes. The spherical sporangia may also become calcified, and may present themselves as rounded

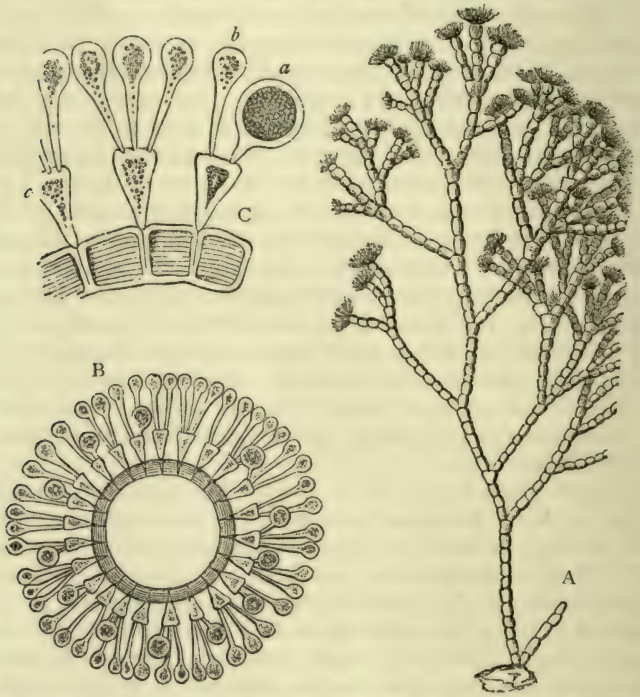


Fig. 1360.—*Cymopolia barbata* (=*C. rosarium*), from the Canary Islands (Recent). A, A specimen of the natural size, showing the divided thallus; B, Transverse section through a segment of the stem, showing a whorl of lateral processes, of which some are sterile and some fertile; C, Part of the same whorl enlarged still further, showing the primary lateral processes (*c*), giving off sterile offshoots (*b*), and spherical sporangia (*a*). (After Schimper and Zittel.)

cavities in the skeleton. Finally, the cylindrical skeleton may be composed of annular segments or may be undivided, according as the axial cell is, or is not, constricted at intervals. In the former case, the segments are often readily capable of separation, and in fossil examples often present themselves as detached calcareous rings.

When the calcareous skeleton is all that is open to our inspection, as in fossil specimens, the transverse canals with their superficial

pores, corresponding with the lateral whorled processes, may very readily be mistaken for the tubes of polypes or the chambers of polythalamous Foraminifera; and the fossil forms of the family were until recently regarded as referable to the animal kingdom. It was first shown by Munier-Chalmas ("Comptes rendus," tom. lxxxv. p. 814, 1877) that the supposed *Foraminifera* described under the names of *Dactylopora* and *Ovulites* were really referable to the *Algæ*, and that, along with many other types, they belonged to the group of the *Siphoneæ verticillatæ*. Palæontologists, in fact, are now acquainted with an extensive series of fossil forms of this remarkable family of *Algæ*, which not uncommonly give rise to very considerable rock-masses, and thus become of geological importance. The oldest type of the *Siphoneæ verticillatæ* is apparently the *Cœlotrochium* of the Middle Devonian of the Eifel; though the nature of this fossil is not absolutely certain. The Carboniferous Limestone of England also sometimes contains numbers of small calcareous cylinders, with a porous surface, which are probably referable to this family; but further investigation is needed before this can be positively asserted. It is, also, not impossible that the organism described by De Koninck from the Carboniferous Limestone of Belgium, under the name of *Monticulipora inflata* — which likewise occurs in the same formation in Britain, and sometimes attains a considerable size—may really be a peculiar type of the *Siphoneæ*. Apart from the above, the first undoubted appearance of forms of this family is in the Permian rocks, in which the genus *Gyroporella* is found. It is, however, in the Upper Trias that the maximum development of the *Siphoneæ verticillatæ* takes place, the limestones of this period being often essentially made up of the cylinders of *Gyroporella* and *Diplopora*, as occurs, for example, in the Bavarian and Tyrolese Alps. Various forms of the group also occur in the Jurassic and Cretaceous rocks, while there are numerous Tertiary types; but the family is at the present day represented by but a few species, and the range of these is very limited.

Among the more important types of the *Siphoneæ verticillatæ* which occur in the fossil state are species belonging to the genera *Cymopolia*, *Larvaria*, *Dactylopora*, *Gyroporella* (with *Diplopora*), and *Uteria*. In *Cymopolia* (fig. 1360) the thallus is branched, and is covered with a hollow calcareous crust, the surface of which shows close-set pores. The lateral processes, sterile and fertile, are developed in whorls, separated by vacant nodes. A living species of this genus is found in the seas of the Canary Islands and West Indies; while the calcareous cylinders of fossil forms occur not uncommonly in the Eocene Tertiary, and were originally described under the name of *Dactylopora*. The genus *Larvaria* is nearly allied to *Cymopolia*, and likewise includes forms—such as *L. eruca* (fig. 1361, A) and

L. annulus (fig. 1361, B)—which were originally described under the name of *Dactylopora*. Existing forms of *Larvaria* are known, and fossil types occur commonly in the Eocene Tertiary, often in the form of separate segments of the calcareous cylinder. *Dactylopora*, as now restricted, includes Eocene and Miocene types, and is also closely allied to *Cymopolia*. *Gyroporella* (including *Diplopora*) comprises types in which the skeleton has the form of a short calcareous cylinder (figs. 1361, E–G), from one to six millimetres in diameter, with two or more rows of pores on each segment of the stem. This genus begins in the Permian rocks, and is so enormously

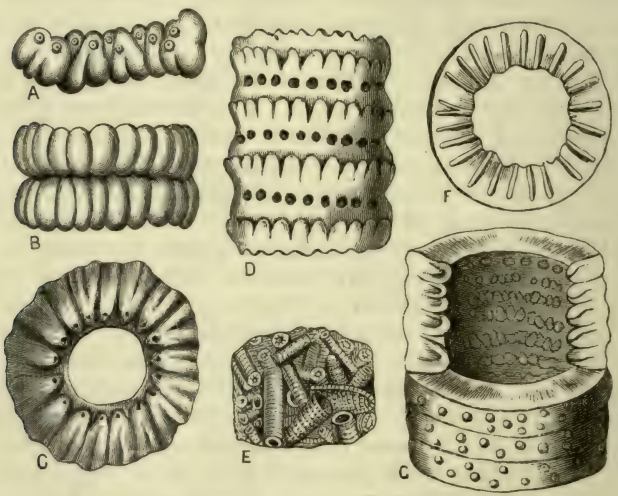


Fig. 1361.—A, *Larvaria* (*Dactylopora*) *eruca* (recent) magnified 30 diameters, and viewed from the inner face; B, *Larvaria* (*Dactylopora*) *annulus*, from the Eocene Tertiary, magnified 40 diameters, viewed in profile, and showing two superimposed rings; C, The same viewed from above and similarly magnified; D, Part of the cylinder of *Dactylopora reticulata* (Tertiary), viewed in profile, and similarly enlarged; E, Fragment of Muschelkalk, with tubes of *Gyroporella cylindrica*, of the natural size; F, Transverse section of a tube of the same, enlarged 10 diameters; G, Vertical section of the same, enlarged 12 diameters. (Figs. A–D are after Carpenter; figs. E–G are after Gümbel.)

developed in the Trias of Southern Germany and Switzerland as to give rise to massive and widespread beds of limestone. A species of this genus also occurs in great numbers in the Cretaceous series of the Southern Lebanon Mountains. In the genus *Ovulites*, again, the skeleton usually presents itself in the form of a small, ovoid or clavate, calcareous body, enclosing a single chamber, with regularly disposed superficial pores, and often perforated at both poles. Such a body is really a single joint of the stem of the original plant. The species of *Ovulites* are found in deposits of Eocene and Miocene age. Lastly, in the genus *Uteria*, the skeleton consists of branched,

cylindrical calcareous stems, which readily separate into their component segments. Each segment is hollow, with smooth or radiately-striate articulating surfaces at its ends; the inner and outer walls being porous, and the space between these being vacant. The detached segments of *Uteria* occur commonly in the Eocene deposits of the Paris basin.

Class V. Florideæ.—This class includes a large number of marine and a few freshwater *Algæ*, which are in general red or violet in colour. The thallus is very variable in form, and is often much branched. Reproduction may be sexual or non-sexual. In the former case fertilisation is effected by means of non-motile antherozoöids, the result being the conversion of the female organ into a receptacle, or "cystocarp," within which spores are formed. Non-sexual reproduction is effected by means of special cells ("tetraspores") developed in parts of the thallus.

With regard to their *distribution in time*, a few types of the ordinary Red Sea-weeds (*Delesseria*, *Sphærococcites*, &c.) have been recognised as occurring in the older Tertiary deposits. With these limited exceptions, all the fossil forms of this class belong to the Corallines and Nullipores (*Corallineæ*), in which the thallus is hardened by the deposition of carbonate of lime. The principal genera of the family of the Corallines are *Corallina*, *Melobesia*, and *Lithothamnion*.

In *Corallina*, the thallus is erect and branched, and is composed of rounded or wedge-shaped calcareous segments, which readily separate from one another. The fructification consists of "cystocarps," which are immersed and have an aperture at their summit. The "Corallines" are exceedingly abundant in existing seas, but little is certainly known of their occurrence in the fossil condition. They are, however, stated to occur in the Eocene beds of the Paris basin.

In *Melobesia* the calcareous thallus is crust-like and foliaceous, and is attached by the whole of its lower surface to foreign bodies. The superficial layer of the stony crust is composed of minute cubical cells, but the deeper cells are elongated. The "cystocarps" are immersed within the thallus, and project above the surface as wart-like tubercles. *Melobesia* has not been clearly recognised in the fossil state, though it is not improbable that it will ultimately be found to occur even in the Palæozoic rocks.

In connection with *Melobesia* a few words may be said about the curious little calcareous bodies known as "coccoliths," since it has been suggested by Carter that these are connected with the reproduction of Algæ belonging to this genus. Coccoliths are excessively minute calcareous bodies, of a discoidal form, which are found in the mud of the deep sea at the present day, often in great numbers. Similar bodies

occur abundantly in the White Chalk, and Gümbel has shown that they are present in many limestones, even in those of the older Palæozoic formations. Two distinct forms of coccoliths are known, which have been described by Huxley under the names of "discoliths" and "cyatholiths." The former of these (fig. 1362, *a*) are minute calcareous discs, averaging $\frac{1}{4000}$ to $\frac{1}{5000}$ inch in diameter, provided with a raised rim on one side (*b* and *c*), and having a central corpuscle or nucleus. The

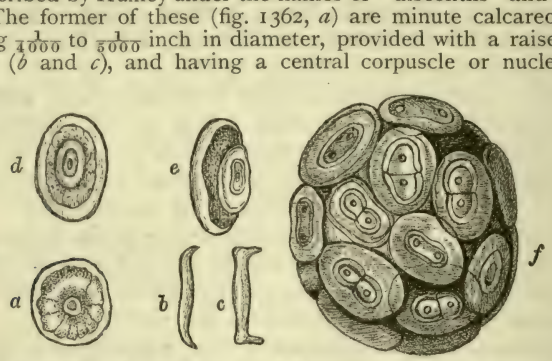


Fig. 1362.—Coccoliths and coccosphere. *a*, A "discolith" seen in front view; *b* and *c*, "Discoliths" viewed edgeways; *d*, "Cyatholith" seen in front view, showing the outer transparent zone, the inner granular zone, and the central corpuscle; *e*, "Cyatholith" seen in profile; *f*, A "coccosphere." All the figures are greatly magnified. (After W. B. Carpenter and Wyville Thomson.)

"cyatholiths" vary from $\frac{1}{1800}$ to $\frac{1}{8000}$ inch in diameter, and when viewed sideways (fig. 1362, *e*) are seen to have the form of a shirt-stud, and to consist of two concavo-convex calcareous discs, of which one is smaller than the other and is united to the concavity of the larger by a short stalk. When viewed in front (*d*), the cyatholith presents itself as an oval or circular body, composed of two concentric zones surrounding an oval central corpuscle, the inner of the two zones being more or less distinctly granular, while the outer one is transparent. Cyatholiths occur in vast numbers in the mud of the deep sea in their detached condition, but they are also found aggregated into spherical masses, which may reach $\frac{1}{700}$ inch in diameter, and are known as "coccospheres" (fig. 1362, *f*). The precise nature of the coccoliths and coccospheres is at present uncertain; but it has been suggested by Carter that the "coccospheres" are connected with the reproduction of species of *Melobesia*.

The only remaining genus of the *Corallineæ* which demands consideration is *Lithothamnion*, under which are included the well-

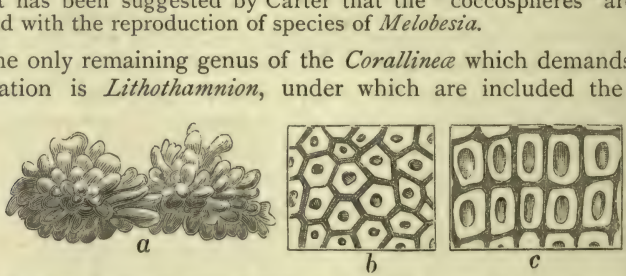


Fig. 1363.—*Lithothamnion ramosissimum*, a "Nullipore," from the "Leitha-Kalk" of the Vienna basin. *a*, Portion of a mass, of the natural size; *b* and *c*, Transverse and vertical sections of the same magnified 320 diameters. (After Gümbel.)

known and widely distributed calcareous *Algæ* which are commonly spoken of as "Nullipores," and which are exclusively marine in

habit. The thallus of the Nullipores is highly calcareous and of stony hardness, and it may be encrusting, botryoidal, stalactitic, or bushy in form (fig. 1363). As regards the microscopic structure of the calcified thallus, the outer layer is formed of hexagonal or quadrate cells of very small size, while the cells of the interior are oblong in shape. The fructification consists of "cystocarps," scattered through the thallus, and either immersed or projecting as tubercles.

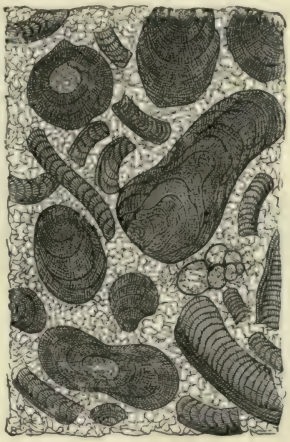


Fig. 1364.—Section of "Leitha-Kalk" (Tertiary) from the neighbourhood of Vienna, showing fragments of Nullipores (*Lithothamnion*), enlarged three times. (Original.)

As regards the distribution of the genus in time, the remains of species of *Lithothamnion* are found in vast numbers in various Tertiary formations, often giving rise to massive limestones, such as the "Leitha-Kalk" of Austria (fig. 1364), the "Nullipore-limestone" of Algeria, and others. Remains of *Lithothamnion* are also found in the Cretaceous and Jurassic rocks, and they have been said to occur in rocks as old as the Carboniferous Limestone. The fossil forms of *Lithothamnion* do not exhibit any marked structural differences as compared with the existing types of the genus.

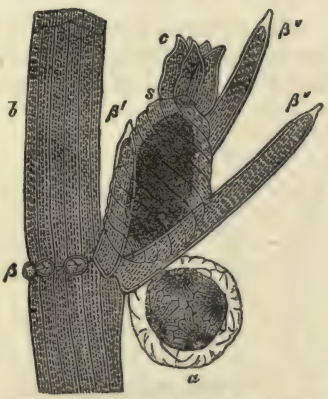


Fig. 1365.—Part of the thallus of *Chara fragilis* (Recent), showing the reproductive organs, enlarged. *b*, Central portion of a leaf with an antheridium (*a*) and a carpogonium (*s*); *c*, Crown of cells at the apex of the carpogonium; β, Sterile leaflets; β', Large lateral leaflet near the fruit; β'', β'', Leaflets attached to the base of the carpogonium. (After Sachs.)

Class VI. Characeæ. — This class comprises a number of fresh-water or brackish-water Algæ, of a green colour, and remarkable for having lateral appendages corresponding with leaves. The thallus consists of a central stem giving off whorls of leaves at intervals, which in turn give off secondary leaflets. The male reproductive organ has the form of a spherical sac (fig. 1365, *a*), and has been sometimes spoken of as the "globule." The female reproductive organ or "carpogonium"—sometimes spoken of as the "nucule"

—consists of a large central cell surrounded by a sheath of spirally-twisted cells, and bearing a crown of small teeth at its summit (fig. 1365, *s*).

The recent genus *Nitella* remains permanently soft, and is unknown in the fossil condition. On the other hand, the integument of *Chara* itself becomes hardened by an encrustation of carbonate of lime, and is thus capable of preservation in the fossil state. The fossil forms of the genus *Chara* occur in the Triassic, Jurassic, and Cretaceous formations, and are abundant in parts of the Tertiary series. In some cases (as in the chert of the Purbeck beds) the stems are found; but the fruits or "carpogonia" are more commonly preserved. These have the form of spirally ridged or grooved, ovoid or globular bodies (fig. 1366), and the first type discovered was described by Lamarck under the name of "Gyrogonites." The fossil carpogonia of species of *Chara* are abundantly found in certain freshwater deposits, both of Secondary and of Tertiary age.

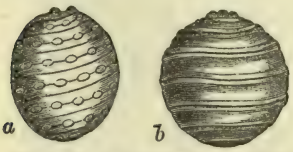


Fig. 1366.—*a*, Carpogonium of *Chara Gressini*, Tertiary, enlarged; *b*, Carpogonium of *Chara Medicaginula* ("Gyrogonites"), from the Eocene beds of the Paris basin, enlarged. (After Schimper and Zittel.)

Fungi.

The series of the *Fungi*, in which the Lichens are now included, comprises Thallophytes which are closely allied to the *Algæ*, but which are devoid of chlorophyll. Owing to the soft nature of their

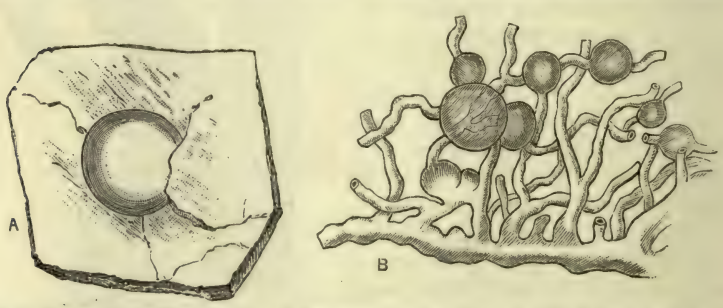


Fig. 1367.—A, A lenticular specimen of *Archagaricon*, of the natural size; B, Slice of the same showing the tubes and vesicles, enlarged. Coal-measures. (After Hancock and Atthey.)

tissues, the *Fungi* can only be preserved in the fossil state under specially favourable conditions. The plants of this series are, therefore, of very small palæontological importance, and may be very briefly dismissed.

Various minute forms of *Fungi* have been recognised as occurring on the leaves of fossil plants, the oldest of these being found on the leaves of Cycads in Triassic deposits. The fossil leaves of Tertiary plants are very commonly attacked by these parasitic plants; and other minute forms have been detected in amber. In other cases, the mycelial tubes of a Fungus have been preserved within the woody stem of a plant of higher grade, or the entire Fungus may have undergone silicification. Thus, the mycelial tubes of a Fungus (*Peronosporites*) have been detected in the tissues of the stems of Carboniferous plants. Messrs Hancock and Atthey have also described, under the name of *Archagaricon*, certain silicified fossils from the Coal-measures of Northumberland, which they regard as referable to the *Fungi*. These remarkable fossils (fig. 1367) present themselves as oval, rounded, lenticular, or irregular bodies, under an inch in length, which appear on microscopic examination to be composed of irregular, ramifying, tubular filaments, terminating in rounded vesicles.

Lichens are almost unknown as fossils, no example of these plants having been detected in any Palæozoic or Mesozoic deposit. A few forms have, however, been recognised in amber, and others have been detected on the bark of fossil trees in lignites of Tertiary age.

CHAPTER LXVI.

SUB-KINGDOM CORMOPHYTA.

Series Bryophyta and Pteridophyta.

Sub-Kingdom B. Cormophyta. — This division, which includes all other plants, can only be distinguished as a whole from the Thallophyta by the general presence of leaves, stem, and root; or at least by the opposition of the stem and root. The alternation of generations is more regular than in the Thallophytes; a sexual production of sporophores, and an asexual production of oöphores, following in sequence.

Series I. Bryophyta.—The first series includes the Mosses and Liverworts, which are cellular plants, with complete alternation of generations, and without true vascular tissue. The spores, either directly, or by the intervention of a *protonema*, give rise to the sexual generation, or *oöphore*, which forms the main plant, in the female organ (*archegonium*) of which arises the *sporogonium* (*sporophore*) from which the spores are asexually produced. The main plant is therefore a sexual oöphore.

Class 1. Musci.—In the Mosses the spore produces a large conferva-like protonema, from which the plant (oöphore) arises by lateral branching, and is differentiated into stems and leaves upon which the sexual organs are formed. The class is practically of no palæontological importance, and it will accordingly be unnecessary to notice its divisions. All the fossil forms at present known are of Tertiary age; but from the occurrence of a Jurassic Beetle allied to types which live in moss, it is inferred that the class is really much older. A number of species have been found in amber, most of which appear allied to existing European types; and some also occur in the Miocene of Bonn and the Upper Eocene of Provence, but the absence of fructification renders their generic position uncertain. The genus *Sphagnum*, or Peat-moss, has, however, been definitely determined from the Miocene of Westerwald.

Class 2. Hepaticæ.—The Liverworts differ from the Mosses in the absence of true leaves, and in the bilateral condition of the plant, which has the side exposed to the light differently organised from the concealed one; the oöphore, moreover, generally arises directly from the spore, the protonema, when present, being insignificant. Hair-like growths, representing aborted leaves, are occasionally present on the under side of the plant; and it is fairly certain that Liverworts are to be regarded as degraded forms which have lost the leaves and branches of the Musci. The widely spread existing genus *Marchantia* is represented in the European Eocene and Miocene, and numerous *Jungermanniaceæ* have been found in amber; but beyond this nothing is known of the palæontological history of the class.

Series II. Pteridophyta.—The Pteridophytes are characterised by the great vegetative development of the sporophore, and the tendency to the suppression of that of the oöphore, or sexual generation. Their tissue develops fibro-vascular bundles, and there is a distinct epidermis. There is also a complete alternation of generations, the spore developing a sexual *prothallium* (oöphore), from the archegonium, or female organ, of which is sexually produced the main plant or sporophore, which in its turn asexually develops spores of one or two kinds in organs termed *sporangia;* the latter being generally borne either on ordinary or specialised leaves, but in some cases on the stem. It will be apparent from this that the main plant is an asexual sporophore corresponding physiologically with the sporogonium of the Bryophytes, while the sexual prothallium represents the leaf-bearing plant of the latter.

The Pteridophytes—equivalent to the Acrogens of older writers—are of extreme importance to the palæontologist, since they contain several groups of entirely extinct types; and in the earlier epoch of the earth's history, when they were not brought into extensive competition with the Phanerogams, they attained an importance, both in the number of types and in the large size attained by many of their representatives, which entitles them to be considered the dominant forms of the Palæozoic epoch.

Class I. Filicaceæ.—The Ferns and their allies have the leaves highly developed, and frequently much branched in a pinnate manner; the sporangia being numerous, and borne either upon the ordinary or specially modified leaves, on which they are usually arranged in groups or *sori*. The class may be divided into three orders.

The leaves of Filicaceæ may be either simple, as in *Glossopteris* (fig. 1376), or pinnate. Among pinnate types the pinnation may be simple, as in *Neuropteridium* (fig. 1373), when the leaflets or pinnules are arranged upon a single shaft; or bipinnate (*Neuropteris*, fig. 1371), when

secondary shafts are developed; tripinnate, as in *Sphenopteris* (fig. 1369), when tertiary shafts occur; or multipinnate. The coverings of the sori are termed *indusia;* and when the stem is creeping it is known as a *rhizome.*

Order 1. Stipulatæ.—This order now contains only the two families *Ophioglossaceæ* and *Marattiaceæ*, characterised by the presence of stipules at the base of the petioles of the leaves. Of the former *Ophioglossum* (Adder's-tongue), in which the sporangia are embedded in the tissue of the partly sterile and partly fertile leaves, occurs in the Middle Eocene of Monte Bolca; while it is probable that *Chiropteris*, of the Keuper of Würtemberg, is not really separable. In the second family, where the sporangia are external, as in the Ferns, the existing genus *Marattia* occurs in the Rhætic and Lias of the Continent. *Danæites* and *Danæopsis*, on the other hand, are extinct types, the former occurring in the Cretaceous of Europe, and the latter in the Keuper, and probably also in the Permian, of the Tyrol, as well as in the Rajmahal stage of the Indian Gondwanas. Finally, the living genus *Danæa* occurs in the Lias of Verona. Several of the fossil forms have been confused with the *Tæniopterideæ*, while Schimper has referred to this family some of the forms noticed under the *Pecopterideæ.* According to Mr Kidston, the *Archæopterideæ* should probably be placed in this order.

Order 2. Filices.—In existing Ferns stipules are wanting; and there is only one kind of spores; so that the sexual stage is not reached till the prothallium.

Existing forms are classified by the nature of their fructification; but since this is generally unknown in the earlier fossil types, we are compelled to classify them by the nature of the pinnation and venation of the leaves, and as these are subject to great variation among allied existing genera, it is evident that this classification is more or less of an artificial nature. It will be convenient to follow Schimper's plan of treating first of those existing families which are known to be represented in a fossil state, and then to notice the forms of which the position is more or less uncertain, but which are provisionally arranged in families.

Existing Families.—In the existing series the family *Osmundaceæ* has the paniculate fructification borne on specialised leaves, which may or may not be like the sterile ones. The type genus *Osmunda*, which is mainly characteristic of warmer regions, although represented in England by the Royal-Fern, occurs fossil in the Cretaceous of Westphalia and Greenland, in the Laramie beds of North America, and in many of the European Tertiaries. An allied form, from the freshwater deposits of Chemnitz, has been named *Asteroclæna.* In the *Schizeaceæ*, which usually have the fructification borne in spikes or panicles on the *laciniæ* of the

leaves, the existing tropical genus *Lygodium* occurs in Europe from the Cretaceous to the Miocene, and also in the Laramie beds of the United States. The third family—*Gleicheniaceæ*—has the sessile sporangia borne in naked sori upon the dorsal surface of ordinary leaves, each sporangium having a complete transverse ring, and bursting with a longitudinal slit; while the stem forms a creeping rhizome. The existing tropical genus *Gleichenia* is represented by closely allied forms in the Cretaceous of Greenland, the Rajmahal group of the Indian Gondwanas, and in the Lias of Verona, some of which have been separated as *Gleichenites*. *Didymosorus*, from the Cretaceous of Greenland and Saxony, with two sori on each leaflet, connects the preceding with *Mertensia*. The latter, which has two rows of sori on each leaflet, and is now confined to the southern hemisphere, occurs in the Cretaceous of Greenland and Hungary. The *Hymenophyllaceæ*, or Film-ferns, in which the sessile sori are covered by an indusium, are represented by one species in the Upper Eocene of Provence; while Schimper has referred to the type genus *Hymenophyllum* a Carboniferous fern. It is probable that some of the *Sphenoptérideæ* are more or less closely related to this family. The fifth family—*Cyathecaceæ*—which includes the tropical Tree-ferns, is of more palæontological importance; it is characterised by the stalked sporangia, situated in closely packed sori, which may be naked or covered. Of Tree-ferns, in which there is a tall stem, often covered with roots, and crowned with a rosette of leaves, the existing *Alsophila* is represented in the Lower Eocene of Sézanne, which also contains other allied forms. The Carboniferous *Choroniopteris* should perhaps find a place here. Of smaller forms, the genus *Onoclea* (in which Schimper includes *Struthiopteris*) is represented in the Laramie Cretaceous and the Miocene of the United States, as well as in the Eocene of the Isle of Mull, by the existing *O. sensibilis* of North America; thus offering a remarkable instance of the persistence of a specific type. The Mull form was originally described as *Filicites*. The Laramie series also yields an extinct species of this genus. These ferns, like the following, have the sporangia borne on specialised leaves. *Dicksonia*, which is mainly tropical and often tree-like, occurs in the European Keuper, and more abundantly in the Jurassic, and is also found in the Indian Rajmahal beds. Finally, *Thrysopteris*, now known only by a single species from Juan Fernandez, is also very common in the European and Siberian Jurassic (fig. 1368), where it has been described as *Coniopteris* and *Tympanophora*. In addition to the special fertile leaves, a few sori are borne at the base of the ordinary leaves, as shown in the figure.

Lastly, we come to the extensive family *Polypodiaceæ*, which includes the greater number of European ferns, and is divided

into several subfamilies. The sporangia are very numerous, and are borne on the underside of usually unmodified leaves; and they split transversely. Of the subfamilies, the *Polypodieæ* are perhaps represented by the typical *Polypodium* in the Miocene of Switzerland; *Chilanthes* occurs in the same deposits; while the widely-spread *Pteris* (Bracken) is found abundantly in the Upper Cretaceous and the Middle and Upper Tertiaries of Europe, and also in the Laramie and Tertiaries of America. *Adiantum* is also equally well represented throughout the European Tertiaries, and if we include in it the so-called *Adiantites*, it ranged down to the Jurassic. In the *Aspleniecæ*, *Blechnum* (Hard-fern), distinguished by having both fertile and sterile leaves, of which the latter are simply pinnate, occurs in the Continental Eocene and Miocene. Curiously enough, the South American genus *Hewardia* is found in the Upper Eocene of Bournmouth. *Woodwardia*, now represented by eight species from the warmer regions of the world, occurs in the Pliocene and Miocene of Europe, the species from the former, and perhaps also that from the latter, horizon being identical with an existing type; this genus also occurs in the Miocene of the United States. *Asplenium*, which at the present day numbers some 300 species, occurs commonly throughout the European Tertiaries, and is also found in the Cretaceous; some of the species being allied to existing European forms, while others are more nearly related to those of the tropics. It appears, moreover, that Ferns from the Jurassic of Siberia and the Jurassic and Rhætic of Europe, described under the name of *Cladophlebis* and *Alethopteris*, are referable to this genus. Ferns of this genus also occur in the English Wealden; in both the Lower (Damuda) and Upper (Raj-

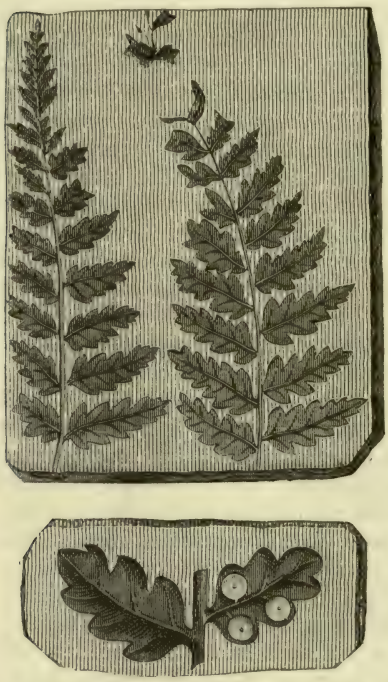


Fig. 1368. — Lateral branches of the leaves of *Thrysopteris Murrayana*; from the Inferior Oolite of Yorkshire. Enlarged leaflets, with sori, are shown in the lower figure.

mahal) Gondwanas of India; and in certain New Zealand beds, correlated by Baron von Ettingshausen with the Trias. In the last subfamily, or the *Aspidieæ*, the cosmopolitan *Aspidium* and the allied *Lastræa* occur commonly from the Middle Tertiaries upwards.

Fossil Families.—An enormous number of Palæozoic and Mesozoic Ferns belong to this series, but only a few of the more important types can be even mentioned. The *Sphenopterideæ* comprise a number of Ferns, mostly of very delicate structure, and extremely difficult to classify. They are usually multipinnate, with the pinnæ in some cases dichotomous; at least the terminal leaflets are narrowed at the base; while all are often lobate, and with the veins dividing in a pinnate or forked manner from the base. The fructification of some forms has been described by Mr Kidston, and it is suggested that one or more of the genera may be allied to the existing *Hymenophyllaceæ*. Many of the species have exceedingly delicate fronds. Among the Carboniferous genera may be mentioned *Sphenopteris* (fig. 1369), *Calymmatotheca*, *Zeilleria*, *Urnatopteris*, in which there are fertile and sterile leaves, *Oligocarpia*, *Renaultia*, *Rhachopteris*, *Sphenopteridium*, and *Eremopteris* (fig. 1370). Of these, the first ranges from the Devonian to the Lower Jurassic of Europe, and is also found throughout a large part of the Indian Gondwanas, in the African Karoo system, in the Australian Hawkesbury beds, in New Zealand, and the Palæozoic of the United States.[1] *Eremopteris* also occurs in the Indian Gondwanas, and ranges in Europe to the Permian; and a Fern from the Kimeridgian of France has been named *Stenopteris*.

Fig. 1369.—Part of a leaf of *Sphenopteris trifoliata*; from the European Carboniferous. (After Schimper.)

The family *Archæopterideæ* (*Palæopterideæ*) was placed by Schimper in the present serial position; but the recent observations of Mr Kidston upon the type genus appear to indicate that it should be transferred to the Stipulatæ—although, until the necessity for such transference be absolutely proved, it appears preferable to leave the family in its old position. The leaves are bipinnate, and both these and the leaflets are usually stalked; the leaflets being broad and often lobate. The type genus *Archæopteris*, which has

[1] Ferns from the Laramie beds and American Tertiaries have been referred to this genus.

also been generally known by the preoccupied name of *Palæopteris*, occurs in the Devonian and Carboniferous of both Europe and the United States. According to Mr Kidston, it has stipules on the leaves, and its fructification appears to consist of sporangia devoid of annuli, and closely resembling those of the *Marattiaceæ*. The genus *Aneimeites*, from the Devonian of Canada, has been placed by Sir J. W. Dawson and Mr Kidston in the same family; which is

Fig. 1370.—*Eremopteris artemisiæfolia*; from the Carboniferous.

also taken to include *Triphyllopteris*, from the European Carboniferous. The latter genus has both fertile and sterile leaves.

With the important family of the *Neuropterideæ* we return to the consideration of true Filices. In this group the leaves vary from a simple to a tripinnate type; the leaflets being either long or ovoid, and often narrowed at the base, with the midrib disappearing towards the extremity, and the veins equal, and in typical forms rising at an acute angle. The genus *Neuropteris* (fig. 1371) is a bipinnate type very common in the Carboniferous, but also extending into the Permian of Europe. The allied *Cyclopteris* (which is not admitted by Mr Kidston as a distinct genus) extends in Europe from the

Carboniferous to the Rhætic, and is also found in the upper part of the Lower Gondwanas of India (fig. 1372). The leaf has sub-

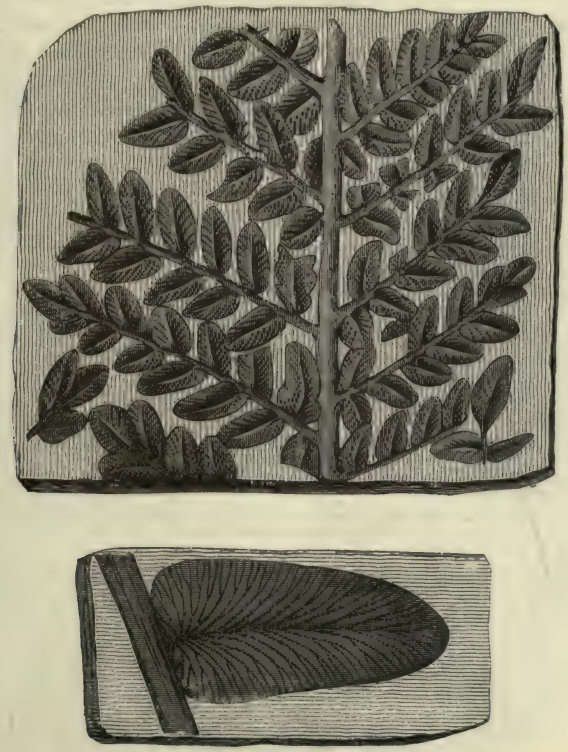


Fig. 1371.—*Neuropteris heterophylla*; from the Coal-measures of Europe. The lower figure shows a single leaflet enlarged.

orbicular leaflets resembling those of the existing Maiden-hair fern, with no midrib, and the veins numerous and dichotomising as they radiate to the margin. The typical Carboniferous forms, according to Mr Seward, have pinnate leaves, but in the figured Rhætic form referred by Dr Feistmantel to this genus they are bipinnate. *Neuropteridium* (fig. 1373) is a simply pinnate form occurring in the Lower Trias of Europe, and in the base of the Lower Gondwanas. *Dictyopteris* includes

Fig. 1372.—Part of leaf of *Cyclopteris pachyrhachis*; from the Panchet stage of the Lower Gondwanas of India. (After Feistmantel.)

Carboniferous ferns with a net-like venation as in *Glossopteris* (fig. 1376). Finally, Mr Kidston includes in this family the simply pinnate *Cardiopteris*, of the Lower Carboniferous, in which the somewhat heart-shaped leaves are devoid of a midrib. The *Odontopterideæ* form a well-defined family with bi- or tripinnate leaves, in which the leaflets are attached by the whole width of their base; the leaflets are non-lobate, with their veins proceeding wholly from the base, or in part from an indistinct midrib. The type genus

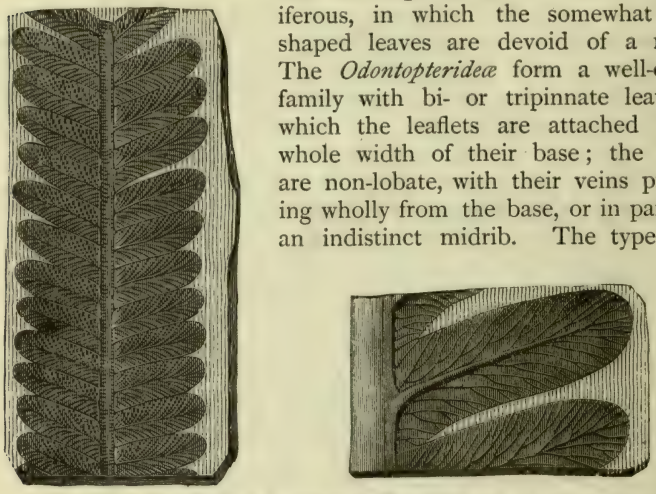


Fig. 1373.—Part of leaf of *Neuropteridium elegans*, and two leaflets enlarged; from the European Trias.

Odontopteris (fig. 1374) occurs in the Carboniferous and Permian, the figured species being common to Europe and North America.

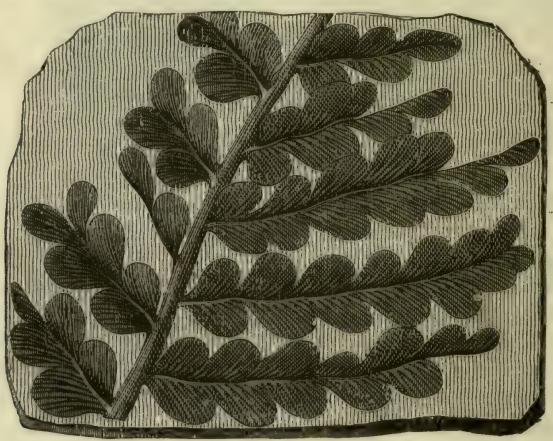


Fig. 1374.—Part of leaf of *Odontopteris osmundæformis*; from the Carboniferous of Europe.

The bipinnate *Ctenopteris* (fig. 1375), from the Rhætic and Lower Lias, has leaves curiously resembling those of the Cycadaceous

Bowenia. The *Alethopterideæ* are multi-pinnate ferns with a strong general resemblance to the existing *Pteris*, and at least some of which have a similar marginal fructification. The leaflets are attached by their whole base, the bases of adjacent leaflets being united; and the midrib is complete. *Alethopteris*, of the Carboniferous and Permian, is common to Europe and the United States; the Mesozoic forms described under this name having been noticed under the head of *Asplenium*. *Lonchopteris*, of the Carboniferous, is distinguished by its net venation; while we have another type in the Permian *Callipteris*. Another multi-pinnate type is constituted by the *Pecopterideæ*, which agree with the last family in the attachment of the leaflets, with the exception that the adjacent bases are usually distinct; the midrib, although slender, continues to the extremity; and the veins arise less obliquely than in the *Neuropterideæ*. The typical *Pecopteris*

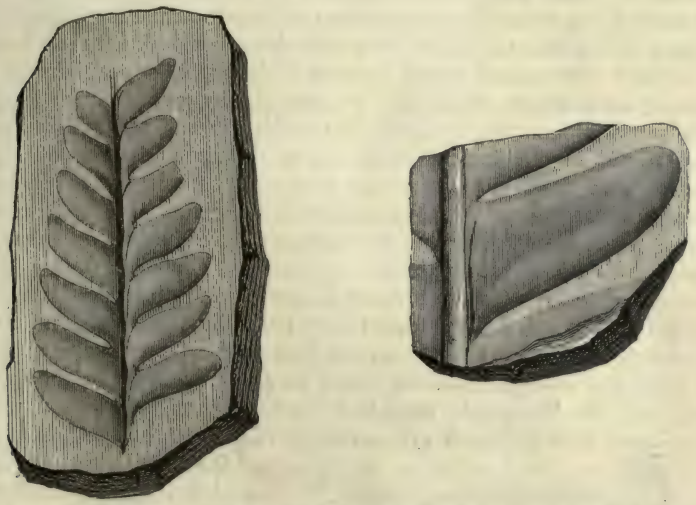


Fig 1375.—A pinna of *Ctenopteris cycadea*; from the Lower Lias. The right-hand figure shows an enlarged pinnule or leaflet.

contains a very large number of species, some of which are tree-like, from the Devonian and Carboniferous of both Europe and North America; and many of which have been referred to the *Marattiaceæ* under the names of *Asterotheca*, *Stichopteris*, &c., but which Mr Kidston considers to be generically inseparable. It also occurs in the Trias of Europe, and in Lower Mesozoic beds in New Zealand. Other Carboniferous genera are *Mariopteris*, *Callipteridium*, and *Dactylotheca*. In the Mesozoic we have also a large number of

forms which may be provisionally placed here, although it is probable that at least a moiety belong to existing families. One series has been named on the evidence of sterile, and the other on that of fertile leaves, and there is accordingly a considerable probability that different genera have been named from a single species. Of the former series a fern from the Keuper and the Panchet series of the Indian Gondwanas has been described as *Pecopteris concinna;* and we also have *Lepidopteris* from the Rhætic, *Merianopteris* from the Keuper and the Damuda series of the Gondwanas, *Anomopteris* of the Keuper, and *Crematopteris* of the Bunter. In the second series, where the leaves consists of palmate branches on a long stalk, we have *Lacopteris*, *Matonidium*, *Marzaria*, *Andriana*, &c. The *Pachypterideæ* are Mesozoic ferns, with small leaves, and include the Liassic *Dichopteris*, and the Oolitic *Scleropteris* and *Stachypteris; Pachypteris* itself being a doubtful form probably based upon remains of two of the preceding genera. The fructification of some of these Ferns resembles that of the existing tropical Polypodiaceous genus *Onychium*, to which they may be allied. In the present family Dr Feistmantel would include *Thinnfeldia*, a peculiar genus having thick leaves, which may be only simply pinnate, with lobate pinnæ; and occurring typically in the Rhætic and Lower Lias, but also found in the Indian Panchets, in the reputed Trias of New Zealand, in the Hawkesbury and overlying beds of Australia, and also in Argentina. The *Lomatopterideæ* include a few Mesozoic ferns of allied types, having thick fleshy leaves, which are usually simply pinnate, with lobation of the pinnæ. Exclusive of the last-named genus this family contains *Lomatopteris*, extending from the Bath Oolite to the Kimeridgian and probably the Wealden; and *Cycadopteris*, which ranges from the Lias to the Upper Jurassic.

With the *Tæniopterideæ* we come to a family easily recognisable by their usually simple strap-like leaves (fig. 1376), with a well-developed midrib, which are curiously like those of the Plaintain (*Musa*). It may be divided into two subfamilies, according to the venation. In the first subfamily, with a normal venation, *Tæniopteris* is represented by a few European and North American Carboniferous species, and also occurs in the Trias of Europe and New Zealand. The allied *Macrotæniopteris* comprises some very large ferns, ranging in Europe from the Keuper to the Lower Lias, and doubtfully to the Inferior Oolite, while it occurs in India in both the Upper

Fig. 1376.—Leaf of *Glossopteris retifera;* from the Lower Gondwanas of India. Reduced. (After Feistmantel.)

and Lower Gondwanas, and is also found in New Zealand and Australia. *Palæovittaria* seems peculiar to the Damuda series of the Lower Gondwanas. *Oleandridium* has stalked leaves differing somewhat in their venation from the preceding, and is considered to be allied to the existing *Oleandra* among the *Aspidieæ;* it occurs in the European Mesozoic and the Panchets. *Angiopteridium* and *Marattiopsis* are distinguished by a simple pinnation of the leaves; the former occurring in the Damuda series of the Gondwanas, and the latter in the European Carboniferous. The genus *Glossopteris* (fig. 1376) is the only representative of the second subfamily, and is distinguished by its net-like venation, retaining, however, the well-marked midrib characteristic of the family. It is extremely abundant in the Indian Gondwanas, ranging from the Talchir to the Upper Jurassic Jabalpur stage, and is also met with in the Hawkesbury beds of Australia, in the upper part of the African Karoo system, in the Cretaceous of Russia, and in beds of unknown age in Italy. Finally, the *Gangamopterideæ*[1] include Ferns with a net venation, in which the leaves are subject to great variation in shape, but may be digitate or fan-like, and devoid of midrib. There is one division with simple, and another with compound venation. In the former we have *Gangamopteris*, ranging throughout the Lower Gondwanas and also found in the Bacchus-Marsh beds of Victoria; and *Belemnopteris* of the *Damudas;* both being probably allied to the *Polypodiaceæ*. In the second group *Camptopteris* occurs in the Keuper; *Dictyophyllum* ranges from the Rhætic of Germany to the Cretaceous of Greenland; while *Clathropteris* is confined to the Rhætic, and *Protorhipis* to the Lias.

Fern-stems.—Omitting a few fossil Ferns of uncertain affinities, brief reference must be made to a few types of large size described upon the evidence of portions of the stem, but which cannot at present be definitely classed. Of these *Megaphyton*, from the Carboniferous of Europe and the United States, is founded on trunks of Tree-ferns, which bore their large leaves in a row on either side of the stem, and which Sir J. W. Dawson considers very unlike any existing type. *Psaronius*—a type common to the Old and New Worlds, and mainly of Devonian age—is founded on trunks of Tree-ferns marked by alternate leaf-scars, which are usually surrounded by aerial roots like those of many existing forms. *Caulopteris*, which is likewise found in both Europe and North America, is characterised by its vertically elongated leaf-scars. It ranges from the Carboniferous to the Permian; but at least some of the forms described under the name of *Ptychopteris*, which extends upwards to the Trias, are not generically separable. *Protopteris*, of the Cretaceous of Europe and Greenland, is another large form,

[1] Usually termed *Dictyopteridæ*, but not including *Dictyopteris* (p. 1507).

characterised by the bases of the leaf-stalks remaining attached to the scars, as in many recent Tree-ferns. Other forms are *Cyatheopteris* of the Bunter, and *Thamnopteris* ranging from the Permian to the Keuper; the latter having persistent leaf-stalks. Finally, *Rhizomopteris* of the Carboniferous, and *Sphallopteris* of the Bunter, are based on specimens generally regarded as rhizomes of large creeping ferns. The genus *Palæopteris*, from the Carboniferous, which was long considered to be a fern, is named from a specimen which appears to be the stem of one of the *Cordaiteæ*.

Order 3. Rhizocarpeæ. — The Rhizocarps are distinguished from the Ferns by the development of two kinds of spores termed *macrospores* and *microspores*. Their young shoots may be either straight, or circinate as in Ferns and *Psilophyton* (fig. 1378).

Although the macrospores and microspores are true spores, as developing plants without fertilisation, yet they may be regarded as incipient sexual elements, and thus throwing back the sexual differentiation to an early stage. Thus the microspores, or male elements, develop only male prothallia, which produce antheridea; while the macrospores, or female elements, develop female prothallia, which produce only archegonia.

The four existing genera of this order are aquatic plants, which may be simply floating, or may have a creeping rhizome. Of the *Salviniaceæ* the rootless genus *Salvinia* is represented in the Upper and Lower Miocene of the Continent, and also in the Laramie and higher beds of America. Of the two existing genera *Pilularia* (Pillworts) and *Marsilia*, constituting the family *Marsiliaceæ*, it is probable that a species of the former occurs in the Upper Miocene of Œningen, while *Marsilia* is recorded from the Miocene of Oregon in the United States, and also from the Lower Miocene of Ronzon near Puy-en-Velay. It has been suggested that *Sagenopteris*, ranging in Europe from the Rhætic to the Lower Jurassic, and also occurring, together with the allied *Dactylopteris*, in the Damudas of India, may be more or less closely allied to the *Marsiliaceæ*. They are plants of considerable size, with long-stalked leaves terminating in a palmate expansion of four or more members. *Marsilidium*, of the Wealden, has also been referred to the same family.

Sir J. W. Dawson considers that in the early Palæozoic the characters afterwards separated in the Club-mosses, Horse-tails, and Ferns were united in the Rhizocarps, and it will accordingly be convenient in this place to notice certain Palæozoic plants apparently more or less closely allied to the Rhizocarps, some of which should probably be included in the same order, while others may be intermediate types connecting that order with the Equisetaceæ and Lycopodiaceæ. In the first place, as previously noted (p. 1484), certain spherical bodies known as *Sporangites* occurring

in the Devonian and Carboniferous of North America and Europe, are regarded by Sir J. W. Dawson as macrospores or sporocarps of Rhizocarps, under the name of *Protosalvinia*. Better known is the genus *Sphenophyllum* (fig. 1377), likewise occurring on both sides of the Atlantic, and ranging from the Ordovician to the Carboniferous, which many authorities now agree in provisionally placing in this order, although others would refer it to the Equisetaceæ. They were small plants with wedge-shaped leaves arranged in regular whorls, after the manner of the existing *Marsilia*. Another type which is regarded by Dr Feistmantel as closely allied to the preceding is *Trizygia*, known by a single species from the Lower Gondwanas of India. These plants (if complete) are comparatively small, with a slender stem bearing incomplete whorls of wedge-shaped leaves; each whorl occupying only three sides of the stem, and consisting of six leaves arranged in three dissimilar pairs. They were probably aquatic.

Fig. 1377.—Leaf of *Sphenophyllum antiquum*; from the Devonian of Canada. Enlarged and natural size. (After Dawson)

Here also, according to Sir J. W. Dawson, should be placed the genus *Ptilophyton* (fig. 1378), which appears to be most nearly

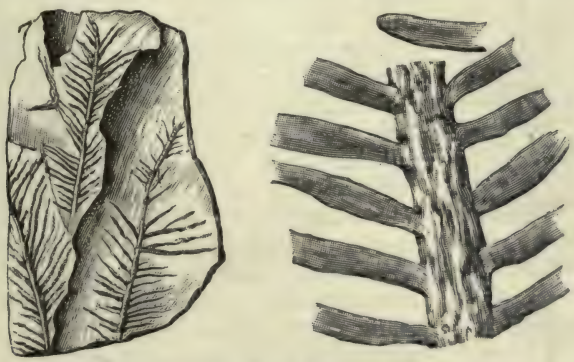


Fig. 1378.—*Ptilophyton plumosum*: from the Lower Carboniferous of Nova Scotia. The right-hand figure shows a portion magnified. (After Dawson.)

allied to the Rhizocarps. The genus ranges in North America from the Middle Devonian to the Lower Carboniferous, and is also found in the Old Red Sandstone of Scotland. These organisms, which have been referred to the Algæ and Lycopodiaceæ, are composed of feather-like leaves, apparently bearing macrospores on parts of the stem or petioles. They are considered to have been of aquatic

habits, the linear pinnæ of the leaves acting as floats. Finally, there remains for consideration the imperfectly-known plants from the Ordovician (Arenig beds) of England to which the hybrid name *Protannularia* has been given; and which were originally referred to the Thallophytous genus *Buthotrephis*. They consist of slender branching stems bearing at intervals whorls of linear leaves (fig. 1379), somewhat resembling those of the Equisetaceæ, to which class they may be more or less closely allied.

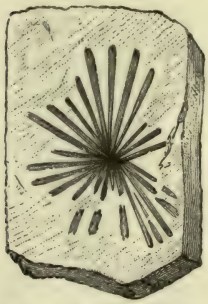


Fig. 1379. — A leaf-whorl of *Protannularia Harknessi*; from the Ordovician of the North of England.

Class II. Equisetaceæ. — With this group we come to a small class now represented by only a single genus with species of comparatively small size, but which in the Palæozoic contained numerous forms of large dimensions, and occupying an important position in the contemporary vegetation. The class may be briefly characterised by the rudimentary condition of the leaves, which are reduced to small sheathing whorls, borne either on the stem or on branchlets also arising in whorls from the joints of the barren stem. The sporangia, which produce only one kind of spores, are borne upon specially modified leaves forming a terminal spike to the main stem (fig. 1381, A), there being distinct fertile and barren stems.

Fig. 1380. — *Schizoneura gondwanensis*; from the Damuda series of India. Much reduced. (After Feistmantel.)

The existing family *Equisetæ* comprises small forms, characterised by their perennial rhizome, from which the annual stems arise. The single existing genus *Equisetum* (Horsetails) occurs in most parts of the world, with the exception of Australasia; and seems to have commenced in the Lower Keuper, where species of much larger size than their existing analogues are met with; and from this period representatives occur throughout most of the European Mesozoic and Tertiary strata and also in some of those of North America, and in the Lower Mesozoic of New Zealand. The Carboniferous *Equisetites* seems to have been an allied genus.

The extinct family *Schizoneureæ* is typically represented by the genus *Schizoneura* (fig. 1380), which occurs throughout the European Trias, and perhaps also in the Jurassic, and in the Lower Gondwanas of India. According to Dr Feistmantel, these plants are characterised by the

sheaths found at the joints of the stalks, which in an early stage of development consist of a number of leaflets, with median veins, and attached by their margins. In the course of development these sheaths split either into thin component leaflets, or more frequently into two equal and opposite portions (as in the figure), which thus simulate paired leaves. The stems and stalks are longitudinally ribbed. *Phyllotheca*, which occurs in Europe from the Lias to the Lower Jurassic, in the Lower Gondwanas of India, and the Newcastle beds of Australia, seems to be more nearly allied to *Equisetum*, but is placed by Schimper in this family. The joints of the stem are of moderate length, and the outer surface is fluted; while the leaves are linear, and free at their extremities, but at the base are united in a sheathing whorl, which may be longer than the joints of the stem. Each leaf has a midrib.

With the *Calamiteæ* we come to another extinct family, which is confined to the Palæozoic, and contains the largest representatives

Fig. 1381. — Restoration of *Calamites*, greatly reduced. A, *C. Suckowii*; B, *C. Cistii*. (After Dawson.)

Fig. 1382. — Leaves and branchlets of *Calamites ramosus* (*Asterophyllites foliosa*); from the Carboniferous of England. Reduced. (After Lindley and Hutton.)

of the class, some of the species probably attaining a height of about 30 feet. Their stems are tall and cylindrical, with a hollow pith-cavity divided into sections by diaphragms, and bearing at the joints either whorls of needle-like leaves (fig. 1381, B), or branchlets carrying secondary whorls of leaves (fig. 1381, A). In transverse section these stems show radiating bundles of fibres,

resembling those of Conifers, and showing great variation of structure in the different forms. The base of the stem generally terminates in a blunt point (fig. 1384), and it may be attached to the rhizome, or several stems may spring from a common stock, as in the restoration figured. The roots are cylindrical, and may be branching. There has been great confusion in regard to the determination of Calamites owing to the difficulty of referring fruits, leaves, and roots to their respective stems; and also owing to the fact that while in some cases the entire stem is preserved, in others only a cast of the pith-cavity remains. According to Mr Kidston the well-defined genera based on stems are *Calamites*, ranging from the Carboniferous to the Permian; *Calamocladus* and *Asterocalamites*, of the Devonian and Carboniferous; and *Arthropitys*, of the Permian. At least some of the specimens to which the names *Annularia* and *Asterophyllites* (fig. 1382) have been applied are branchlets of *Calamites*. Fruits of *Asterocalamites* have been described as *Pothocites;* while others known as *Stachannularia* have been found attached to the branchlets of *Annularia*. Other fruits described as *Volkmannia*, *Calamostachys*, and *Macrostachya* are probably likewise referable in many instances to *Calamiteæ*, although it has been suggested that some may belong to *Sphenophyllum*. Roots known as *Pinnularia* have been found attached to *Calamites*, but some of the specimens to which this name has been applied may belong to other plants. There has been considerable discussion as to the nature of the outer surface of the bark of *Calamites*, but it appears from the most recent observations that in species with thin bark this surface was fluted, while in those with thick bark it was smooth.

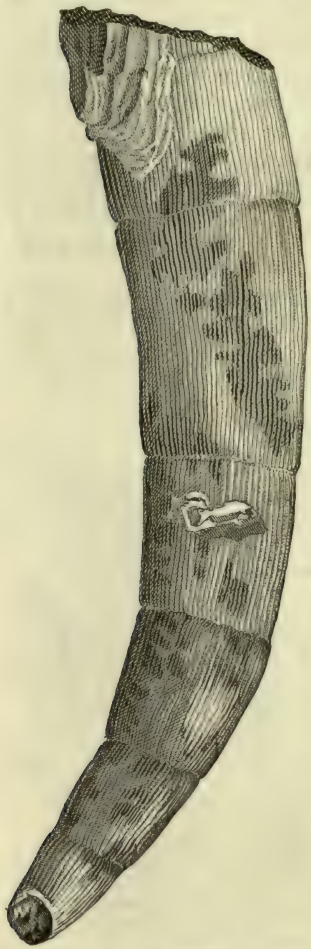


Fig. 1383.—Part of stem of *Calamites cannæformis;* from the Carboniferous of Europe. Reduced.

A large number of synonyms in addition to those already mentioned have been made; among which it may be observed that Mr Kidston includes *Asterophyllum*, or *Asterophyllites*, and *Archæocalamites* in *Asterocalamites;* while *Calamodendron* is regarded as inseparable from the type genus. *Calamiteæ* occur both in Europe and North America, but are unknown in India and Australia.

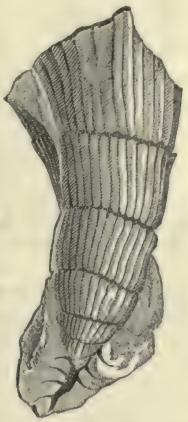


Fig. 1384.—Lower extremity of stem of *Calamites cannæformis;* from the European Carboniferous. Reduced.

According to Sir J. W. Dawson, "it would seem, from the manner in which dense brakes of these Calamites have been preserved in the coal-formation of Nova Scotia, that they spread over low swampy flats, and formed fringes on the seaward side of the great Sigillaria forest. In this way they no doubt contributed to prevent the invasion of the areas of coal accumulation by the muddy waters of inundations, and thus, though they may not have furnished much of the material of coal, they no doubt contributed to its purity."

Here may be noticed the remarkable jointed stem-like bodies known as *Vertebraria*, which are generally regarded as Equisetaceous, and occur throughout the Lower Gondwanas of India, and are also found in the Newcastle beds of Australia. These peculiar bodies, which are often branched, and may be of considerable size, are regarded as the rhizomes of an Equisetaceous plant of which the foliage is unknown. Their association in India with *Schizoneura* is noteworthy.

Class III. Lycopodiaceæ.—The third and last class of the Pteridophytes, known as Lycopodiaceæ or Dichotomeæ, is now represented by the Club-mosses and Selaginellas, and also includes a number of allied extinct types of much larger dimensions. These plants are characterised by a simple or branched stem, without joints, usually having roots, and bearing numerous small and simple leaves; while the branches of the stem and frequently of the roots divide dichotomously (fig. 1387). The sporangia are solitary, and borne either upon the upper surface of the base of the leaves, or in the axils of the latter, or simply upon the stem. The class may be divided into two orders.

Order 1. Isosporeæ.—The Club-mosses, which are the existing representatives of this order, are characterised by producing only one kind of spores, and by the absence of *ligulæ*, or membranes at the base of the leaves, as well as by certain other points which need no mention here.

The earliest plant referred to this order is *Psilophyton*, which is

regarded by Sir J. W. Dawson as forming a connecting link between the Rhizocarps and the Lycopods, and probably forms the type of a distinct family, the *Psilophyteæ*. This genus, with which *Haliserites* is identical, occurs in the Lower Devonian of both Europe and the United States, and is a plant of more than average interest. It attains considerable dimensions, and has minute or rudimental leaves, which are numerous and spirally arranged on the barren stems, but are sparse or absent on the fertile ones. On decorticated stems their point of attachment is represented by minute scars. The young branches have circinate terminations (fig. 1385), like the "crosiers" of Ferns; while the rhizomes are circular, and show irregularly placed areolæ, to which the roots were attached. The inner structure of the stem consists of an axis of scalariform tissue, surrounded by cells. Finally, the fructification (fig. 1386) consists of naked oval sporangia, generally borne in pairs on lateral or terminal pedicels, which are regarded by Sir J. W. Dawson as making the nearest approach to the sporocarps of the Rhizocarps. *Arthrostigma*, from the Devonian of Canada, is placed by the same authority in this family.

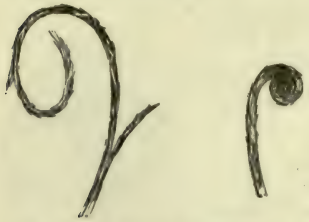


Fig. 1385.—Circinate terminations of young branches of *Psilophyton princeps*. (After Dawson.)

Fig. 1386.—Reduced restoration of *Psilophyton princeps*; from the Lower Devonian of Canada. (After Dawson.)

The three existing families of the order—viz., *Lycopodieæ*, *Psiloteæ*, and *Phylloglosseæ*—are of but little palæontological importance; the last two being unknown in a fossil condition. *Lycopodium* occurs in the Jurassic; while in the Permian, Carboniferous, and Upper Devonian there occur allied forms for which the name *Lycopodites* has been proposed. The Devonian *L. Milleri* is, however, a *Psilophyton*. *Lycopodites* also occurs in Lower Mesozoic beds in New Zealand.

Order 2. Heterosporeæ (Ligulatæ).—This order, now represented by *Selaginella* and *Isoëtes*, is distinguished by developing two kinds of spores—viz., macrospores and microspores—and by the presence of ligulæ to the leaves. In both the prothallium is developed within the

macrospore; thus almost suppressing the first or sexual generation. The family *Selaginelleæ* includes only the living genus *Selaginella*, which is mainly characteristic of the warmer regions, and especially of the southern hemisphere. The stem is flattened, with two

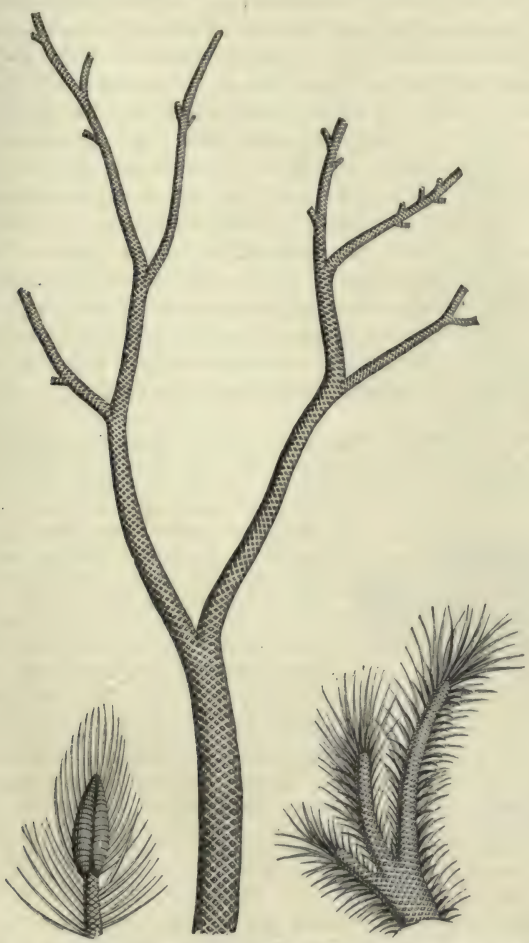


Fig. 1387.—*Lepidodendron Sternbergi*; from the Carboniferous. The left-hand figure shows a cone, and the right the extremity of a branch.

opposite rows of leaves, which are often of a glaucous hue, and the fruit is in the form of long spikes, arising from the axils of the leaves. It is considered probable that this genus is represented in the Coal-measures of the Continent by species which have been

referred to *Lycopodites*, and it undoubtedly occurs in the Laramie series of North America.

With the *Lepidodendreæ* we come to the first of the two extinct families of the order, which contains gigantic forms characteristic of the Upper Devonian and Carboniferous. These were tree-like Lycopods with linear single-veined leaves, which leave rhomboidal scars, often very prominent, at their point of attachment to the dichotomously-branching stems. The fruit is in the form of scaly cones, bearing macrospores and microspores, which may be either terminal or lateral; and the young branches have a pith-cavity, surrounded by a layer of scalariform tissue, which sends out processes through the thick bark to the leaves. As is the case with so many Palæozoic types, the different portions of these trees have received distinct generic names. Thus the decorticated stems have been named *Knorria*, fruiting branches, *Halonia*, and cones (fig. 1388) *Lepidostrobus*, while at least some of the roots known as *Stigmaria* (fig. 1392) are referable to the present family. According to Sir J. W. Dawson, there is considerable difference in the mode of growth of the outer surface in different members of the family.

"Thus in some species the areoles, at first close together, become, in the process of the expansion of the stem, separated by intervening spaces of bark in a perfectly regular manner; so that in old stems, while widely separated, they still retain their arrangement, while in young stems they are quite close to one another. This is the case in *Lepidodendron corrugatum*. In other species the leaf-scars or bases increase in size in the old stems, still retaining their form and their continuity to one another, as in *L. undulatum*, and those forms which have large leaf-bases. In these species the continued vitality of the bark is shown by the occasional production of lateral strobiles [cones] on large branches, in the manner of the modern Red-pine of America. In other species the areoles neither increase in size nor become regularly separated by growth of the intervening bark; but in old stems the bark splits into deep furrows, between which may be seen portions still retaining the areoles in their original dimensions and arrangement."

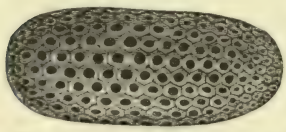


Fig. 1388.—Cone of a Lepidodendroid Tree (*Lepidostrobus Dabadianus*); from the Carboniferous. One-third natural size. (After Schimper.)

The majority of the genera are common to Europe and the United States, and some of them occur in other parts of the world, as in the Palæozoic of Australia, and the *infra*-Karoo series of South Africa. The type genus *Lepidodendron* contains a number of species with a most complex synonomy, and is characterised by its vertically elongated leaf-scars and slender branches. According to the views of Mr Kidston, the stems to which the name *Ulodendron* has been applied are mainly referable to *Lepidodendron*, although others may

be Sigillarian; Sir W. Dawson has, however, identified *Ulodendron* with the next genus. *Lepidophlœus* (*Lomatophlœus*), which appears to be exclusively Carboniferous, has the leaf-scars transversely elongated, with three vascular points, and placed on distinct prominences; while the branches are thick, the leaves very long, and the cones always lateral. *Hallonia* is founded on fruiting branches of this genus; while fruits of one type of the so-called *Lepidostrobus* (fig. 1388) have been found attached to stems with the scars of *Lepidophlœus*. *Cyclostigma* and *Leptophlœum* are exclusively Devonian; the former being characterised by the circular or horse-shoe-like leaf-scars, and the latter by the flat and rhombic leaf-bases and obsolete scars. *Leptophlœum* occurs in the United States and Australia.

The existing genus *Isoëtes*, the sole representative of the *Isoëteæ*, is known in a fossil condition by two species from the Miocene of the Continent, and by a third from the Eocene of Colorado.

With regard to the serial position of the second great Palæozoic family of the *Sigillareæ*, there has been much discussion, but the general consensus of opinion seems now to be in favour of placing them in the present order; although it is quite probable that, as Sir J. W. Dawson suggests, at least some of them may be more or less closely allied to the primitive Gymnosperms. Their resemblance to the *Lepidodendreæ* is indicated by their strongly-marked external similarity; which is especially shown in the tall, slender, and dichotomously-branching stem (fig. 1389), the slender grass-like leaves, the leaf-scars arranged in whorls, and the Stigmarian roots. These trees, constituting the genus *Sigillaria*, are mainly of Carboniferous age, and are common to the Old and New Worlds; they attained very large dimensions, their stems being sometimes as much as five feet in diameter. Not unfrequently these stems are found in an erect position (fig. 1390), passing through several layers of rock; while in other cases they have been found attached to the Stigmarian roots which penetrate the clays underlying the seams of workable coal. The columnar

Fig. 1389.—A, Reduced restoration of *Sigillaria Browni*; B, Do. of *S. tessellata*; from the Carboniferous. (After Dawson.)

stems of the Sigillarians are marked by continuous longitudinal ribs, between which are the leaf-scars (fig. 1391), forming whorls round the stems. It will be seen from the figure that the arrangement of these scars is such that each one is placed in the interval between two scars of the horizontal rows immediately above and below; this arrangement, or *phyllotaxis*, obtaining in all plants with leaves forming whorls. The external coat of the stem is very hard, beneath which is an inner bark composed of cellular tissue traversed by rope-like fibres, while the woody central axis is small, and somewhat intermediate in structure between that of the Lepidodendroids and Gymnosperms. The roots (*Stigmaria*) usually start from the stem in four main branches, which divide dichotomously several times, and then continue in long extensions, which Sir J. W. Dawson considers are

Fig. 1390.—Stem of a semi-erect *Sigillaria* in a coal-seam; from Nova Scotia. (After Dawson.)

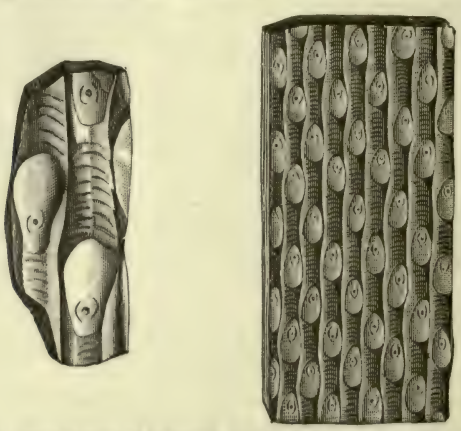


Fig. 1391.—Part of stem of *Sigillaria Utschneideri*; from the Carboniferous. The left-hand figure shows a small portion on a larger scale.

intended to afford a firm support in a soft marshy soil. The rootlets (fig. 1392) were arranged on the roots in whorls; and when

they decayed they left scars on the bark (figs. 1392 and 1393) corresponding to the leaf-scars on the stems. The nature of the fruit is still unknown, but it is probable that it more or less closely resembled that of the Lepidodendroids. Sir J. W. Dawson has, however, suggested that some of the Sigillarians may have had

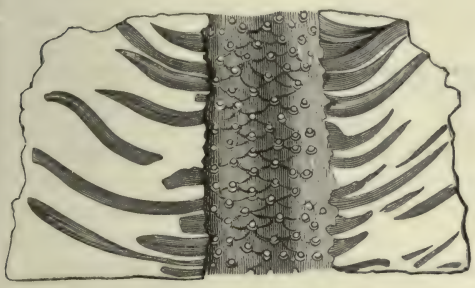


Fig. 1392.—Part of root of a Sigillarian or Lepidodendroid Tree (*Stigmaria ficoides*); from the Carboniferous. One-quarter natural size.

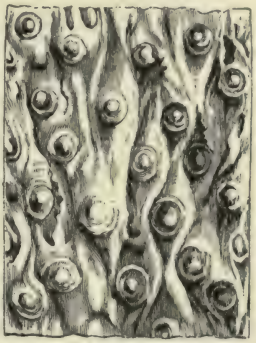


Fig. 1393.—Bark of a Sigillarian or Lepidodendroid root; from the Carboniferous. (After Dawson.)

fruit of the type of *Trigonocarpus* (fig. 1400), and that such forms consequently exhibit a connecting link between the Pteridophytes and the Gymnospermous Phanerogams.

The genus may be divided into several groups, which may eventually have to be raised to generic rank. The Clathrarian group (in which Mr Kidston includes some species of *Ulodendron*) has a thin bark, with the leaf-scars not in distinct rows, but having a spiral appearance; type, *S. discophora*, of Europe and the United States. In the Liodermarian group the ribs on the bark are obsolete, and the leaf-scars in distinct rows; type, *S. sydnensis*, of Australia. In the third, or Rhytidolepidian group, in which the Favularian group may be included, the ribs are narrow (fig. 1391) and often striate, and the leaf-scars large and hexagonal, or shield-shaped; type, *S. tessellata* (fig. 1389, B). Finally, the typical group is characterised by the broad ribs to the bark, of which the width usually exceeds that of the oval or elliptical leaf-scars; types, *S. reniformis* and *S. Browni* (fig. 1389, A).

CHAPTER LXVII.

SUB-KINGDOM CORMOPHYTA—continued.

SERIES PHANEROGAMÆ.—CLASS GYMNOSPERMÆ.

SERIES III. PHANEROGAMÆ.—The Phanerogams, which include the whole of the remaining groups of plants, are characterised by the production of a seed, and the consequent concealment or compression of the alternation of generations. It has already been mentioned that in several groups of Pteridophytes the tendency of the oöphore (prothallium) is to lose its independent existence, but in the present series this independence is totally suppressed. Thus the macrospore or female element, now termed the *embryo-sac*, is never detached from the main plant, or sporophore, previous to fertilisation; while the oöphore, now known as the *endosperm*, which may be rudimentary, is always enclosed in the macrospore (embryo-sac). The seed is developed from the *ovule* (of which the envelope is known as the *testa*), which produces the embryo-sac, and in this the endosperm and the *oösphere*. The latter is fertilised by the *pollen-tube* or outgrowth from the *pollen-grain*, which represents the microspore of the Pteridophytes.[1] The plant is always differentiated into stem, leaves, roots, and hairs; and its branching is normally monopodial, the main axis continuing to grow and producing its lateral shoots and roots beneath its apex. Phanerogams are further characterised by the metamorphosis and differentiation of homo-

[1] It is thus evident that the Phanerogam with its pollen-grains and embryo-sacs is equivalent to the sporophere of the Pteridophytes. The sexual differentiation, which in the most specialised members of the latter commences with the formation of macrospores and microspores, is, however, carried further back, being manifested not only in the formation of embryo-sac and pollen-grains, but also in the differences between ovule and pollen-sac, and between the modified leaves (*carpels* and *stamens*) bearing them, and, even earlier, in the distinction between male and female flowers, and finally in the development of separate male and female (*diœcious*) plants. At least for a time, the seed unites in itself the two generations—the prothallium (endosperm), and the embryo or young plant of the second generation. (Sachs.)

logous structures for the purpose of reproduction, as is shown in the flower, into the complex structure of which it will be unnecessary to enter here. The differentiation of the tissues is also more complex than in the Pteridophytes.

Phanerogams include the highest types of plant life, and it will be seen from the sequel how there has been a gradual advance in their degree of organisation as we ascend in the geological scale; the most specialised groups only making their appearance at a late epoch.

Class I. Gymnospermæ.—The first and most generalised class of Phanerogams is characterised by the ovules and seeds not being enclosed in the ovary, and by the early development of a distinct endosperm forming archegonia in which the oöspheres originate. The first leaves produced from the embryo are arranged in whorls of two or more; and the wood grows from the outside, forming annual rings of growth.

In many respects the existing Gymnosperms are intermediate between the Pteridophytes and the Phanerogams; and it is practically certain, as we have already hinted, that in past times there was a complete transition between the two series. The class includes the Cycads and Conifers and dates from the Devonian; but in the middle Mesozoic, which has hence been termed the "age of Gymnosperms," it attained its highest stage of development, and constituted the dominant type of the flora. The existing forms are usually arranged in three orders, while a fourth is frequently made for the reception of the extinct *Cordaites*.

Order 1. Cycadaceæ.—Existing Cycads (fig. 1394), which occur in the warmer regions of America and Asia, and also in South Africa

Fig. 1394.—A male Cycad (*Macrozamia spiralis*); from Australia. Greatly reduced.

and Australia, are low palm-like trees, with a short unbranched stem, occasionally divided into two, marked by leaf-scars. The leaves form a crown, and, except in one genus where they are

bipinnate, are simply pinnate; their structure is very firm, and they usually develop in a circinate manner like ferns. The plants are male and female; the male fructification being borne in cones (fig. 1394), while in the female the ovules are usually situated on the margin of modified leaves or on the base of scales.

Existing Cycads are divided into the families *Cycadeæ*, *Encephalarteæ*, *Stangerieæ*, and *Zamieæ*. Of these the living South African genus *Encephalartos* occurs in the Miocene of Eubœa, and perhaps in the Rhætic of Honduras; while a leaf from the Miocene of Styria has been referred to the Mexican genus *Ceratozamia*, belonging to the *Zamieæ*.

The family position of extinct genera is for the most part uncertain, and it is accordingly unadvisable to make any attempt at such divisions. As is usually the case with fossil plants, genera have been founded upon different portions of the organism, so that in many cases we doubtless have the same type described under two or more names. In the Mesozoic, as Sir J. W. Dawson remarks, Cycads had a world-wide distribution, and many of the undermentioned European genera likewise occur in America. The species occurring in the Cretaceous of Greenland are, according to the same authority, of small size and low growth, so that they may have been protected from the winter snows. Some of the more southern forms attained, however, a considerable height, and must have resembled palms. The order is known from the Carboniferous upwards.

Genera founded on Leaves. — The genera based on the evidence of leaves will be taken first. Of these *Cycadites* has the leaflets attached by the whole width of their base to the stem, with a single vein, while the young leaves are circinate; in all of which respects it approximates to the existing *Cycas*. It occurs in Europe from the Carboniferous to the Upper Cretaceous; and in India it is characteristic of the Upper Gondwanas. *Podozamites* with small leaves, and the leaflets alternating and narrowed at the base, ranges in Europe from the Rhætic throughout the Jurassic and into the Lower Cretaceous; it is also found in the Dakota Cretaceous, in the Upper Gondwanas of India, and in the reputed Trias of New Zealand. Till something is known of its fructification the affinities of this genus cannot be determined. *Zamites*, again, is a very large genus with small or medium-sized leaves, in which the leaflets are attached by a calus to the upper surface of the stem, and are subject to a considerable variation of form. In Europe this genus is well represented from the Middle Trias to the Upper Cretaceous (Greenland), an isolated species being found in the Miocene. It is also recorded from the reputed Trias of New Zealand, and the Upper Gondwanas of India. *Glossozamites* includes large-leaved Cycads with subsymmetrical leaflets, occurring typically in the European

Wealden, but according to Dr Feistmantel also represented in the Lias and the Lower Gondwanas of India. *Ptilophyllum* (fig. 1395) is a genus characteristic of the Upper Gondwanas, having long narrow leaves, with alternating leaflets which are likewise long and narrow, and are attached to the front of the stem, with upwardly-directed terminal points, and a simple venation. *Otozamites* (fig. 1396),

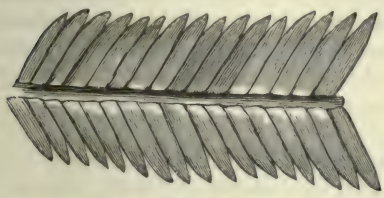


Fig. 1395.—Part of leaf of *Ptilophyllum cuchense*; from the Upper Gondwanas of India. (After Feistmantel.)

Fig. 1396.—Part of leaf of *Otozamites bengalensis*; from the Lower Gondwanas of India. (After Feistmantel.)

according to the last-named writer, is allied to *Ptilophyllum*, but distinguished by the lower basal angle of the leaflets, which in the latter is affixed and decurrent on the stem, becoming free and rounded like the upper one; the disposition of the veins being very similar in both genera. In Europe this genus occurs very abundantly from the Rhætic to the Upper Jurassic, is well represented in the Cach stage of the Upper Gondwanas of India, and also occurs in the Rhætic of Honduras. *Ctenophyllum* is an allied genus typically from the Upper Lias and Lower Jurassic of Europe. An important genus is *Pterophyllum*, in which Dr Feistmantel includes *Anomozamites* of Schimper, occurring in Europe from the Carboniferous to the Upper Jurassic and Wealden, in India from the higher stage of the Lower Gondwanas to the two lower divisions of the Upper Gondwanas, and also recorded from the reputed Trias of New Zealand. The leaves are stalked, of moderate size, and considerable width; while the leaflets are generally opposite, articulating at right angles with the sides of the stem, and having numerous veins. *Ptilozamites* is an allied type from the Rhætic of the Continent. *Nilssonia*, of the Rhætic and Lower Jurassic of Europe, is readily distinguished by its leaves being either strap-like and undivided, or with slight segmentation. *Sphenozamites* from the French Jurassic and the Rhætic of Honduras, and *Macropterygium* from the Keuper of Carinthia, are imperfectly known forms which may be allied to *Nœggerathia* noticed below. *Dictyozamites* is a peculiar form from the Upper Gondwanas characterised by the leaves having a net-like venation, as in the genus *Glossopteris* (fig. 1376) among the Ferns, and is regarded by Dr Feistmantel as the type of a distinct family. Another type is presented by the genus

Rhiptozamites from the Jurassic of Siberia, to which *Nœggerathiopsis* of the Lower Gondwanas of India, the Hawkesbury beds of Australia, and the Rhætic of Honduras, is closely allied, if indeed it be generically separable. It is known by specimens which appear to be leaflets of a pinnate leaf, and are of an elongate form with forked radiating veins which do not converge towards the summit.

Genera founded on the Fructification.—The name *Cycadospadix* has been applied to the female fructification of Cycads from the Lower Lias and Corallian closely resembling that of *Cycas*. Cones from the Lias to the Wealden have been described as *Zamiostrobus* and *Beania;* while seeds, ranging from the Keuper to the Wealden, are known as *Cycadeospermum*.

Genera founded on Stems.—Stems of Cycads are of not uncommon occurrence, especially in fresh-water deposits, and are locally known to the quarrymen of the south of England as "fossil birds'-nests." According to the arrangement of Count Saporta they may be classified as follows: *Bolbodium*, from the Lias and Corallian; *Cylindropodium*, from the Lower Lias and Upper Jurassic; and *Mantellia* (fig. 1397), also known as *Cycadoidea* or *Clathropodium*, from the Upper Jurassic and Wealden, which is especially common in the "dirt-bed" of the Isle of Portland. Other stems, ranging from the Jurassic to the Lower Greensand, have been described by Mr Carruthers under the name of *Bennettites;* the associated fructification differing in several respects from that of existing types. The preceding forms have comparatively short stems, but in *Platylepis*, of the Lias, and *Fittonia* and *Bucklandia*, of the Upper Jurassic and Wealden, the stems may attain a height of several feet.

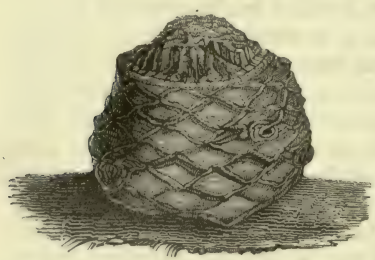


Fig. 1397.—Stem of *Mantellia megalophylla;* from the Purbeck of the Isle of Portland. Reduced.

Here we may notice the remarkable genus *Williamsonia*, ranging from the Rhætic to the Jurassics of Europe, in regard to the serial position of which there has been much discussion. It is based on the fructification, which in some cases is found attached to stems with spirally arranged leaves. It has been suggested that this plant may belong to the Dicotyledons, while Mr J. S. Gardner considers that its affinities are with the monocotyledonous *Pandanaceæ;* but it appears quite possible that it may really prove to be an extremely aberrant Cycad. This genus is also found at the base of the Upper Gondwanas of India.

Transitional Types.—The families *Nœggerathieæ* and *Cordaiteæ*, of the Palæozoic, appear to include types which are in many respects transitional between the existing Cycads and Conifers, and may therefore provisionally occupy an intermediate position. Both families are, indeed, referred by Mr Kidston to the Cycads, but other writers would place some or all of these forms with the Conifers. In the first family the type genus *Nœggerathia*, which occurs in the European and North American Carboniferous, has the leaves arranged in two opposite rows (distichous), these

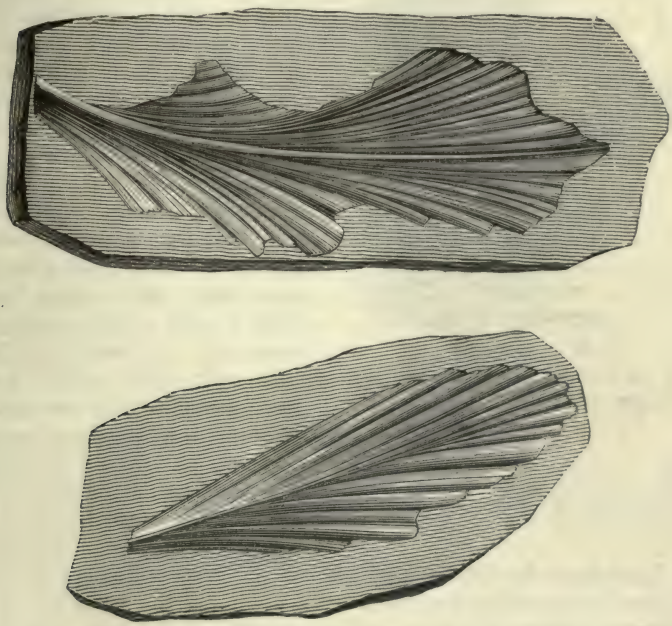


Fig. 1398.—Leaves of *Psygmophyllum expansum*; from the Permian of Russia.

leaves having a cuneiform base, with radiating veins which do not form forks. *Psygmophyllum* (fig. 1398), or *Gingkophyllum*, is an apparently allied type from the European Carboniferous and Permian, which is placed by Dr Schenk with the Taxoid Conifers. A branch from the upper Devonian of Wyoming, described by Sir J. W. Dawson as *Dictyocordaites* is stated to connect *Nœggerathia* with the under-mentioned genus *Cordaites*; since, in place of the parallel venation of the latter, the veins fork at an acute angle, and are slightly netted by the spreading branches of one vein uniting with those of an adjacent one. The

second family is represented by the genus *Cordaites* (fig. 1399), ranging from the Devonian to the Permian, and occurring in both the Old and New Worlds. These plants formed trees reaching to a height of 20 or 30 feet, with the stems marked by transverse leaf-scars, and the leaves arranged in whorls; the leaves themselves (fig. 1399) being comparatively broad, with parallel longitudinal veins, and attached by a somewhat wide base. Their fructification consisted of male and female catkins, forming long racemes (fig. 1399), and known as *Antholithus;* which subsequently produced berries known as *Cardiocarpus*, some of which appear to have had wing-like envelopes, while other types had a soft pulpy cover like those of the existing Yews. The stem had a large central pith surrounded by scalariform tissue with a cylinder of woody wedges; the casts of these pith-cavities are included among the so-called *Sternbergia*, to be shortly mentioned. According to Dr Schenk the female fructification of *Cordaites* is most like that of the Cycads, while the male fructification and the structure of the stem comes nearest to the Conifers.

Fig. 1399. — A branch of *Cordaites;* from the Carboniferous. Reduced. (After Grand' Eury.)

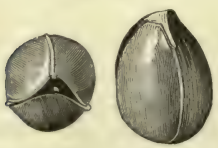


Fig. 1400. — *Trigonocarpus Parkinsonsi;* from the Carboniferous of England. (After Lindley and Hutton.)

In this place certain Carboniferous fruits which have not at present been referred to their respective plants may be conveniently noticed. These have been named *Rhabdocarpus*, *Carpolithus*, *Trigonocarpus* (fig. 1400), and *Palæoxyris*. They are large and angulated nut-like fruits, resembling those of the Yews. Specimens of *Trigonocarpus* are extremely numerous in some of the coal-measures; a slab of sandstone in the British Museum measuring 21 × 15 inches containing more than 400 of these nuts. The sug-

gestion of Sir J. W. Dawson that some of these fruits may belong to Sigillarians has been already mentioned, but most recent authorities agree in regarding them as belonging to *Cordaiteæ* or Conifers.

Order 2. Coniferæ.—This order includes the existing Yews, Pines, and allied forms, and is of considerable palæontological importance, although the different groups can be but very briefly mentioned in this work. Conifers are characterised by the strong and continuous growth of the main axis, which forms a slender conical stem sometimes exceeding 200 feet in height; on this main stem the lateral axes, or primary branches, arise either in rosettes at intervals, or irregularly, and again subdivide in the same manner; the whole contour of the tree thus forming a more or less regular cone. The leaves may be either all foliage leaves containing chlorophyll; or all colourless or brownish scales; or a mixture of foliage leaves and scales. The foliage leaves are mostly small and simple, and very rarely compound; and thus form a striking contrast to the Cycads, where the leaves constitute the greater part of the plant. The flowers are always of separate sexes; but the trees themselves may either bear one or both kinds of flowers. These flowers are never terminal on the main axis, and are subject to great variation of structure in the different families. The male flowers are not of much importance to the palæontologist, who has more often to deal with those of the female. The best known examples of the latter are the cones of the *Abietineæ*, which are modified shoots bearing a number of closely packed woody scales, on which the ovules are usually placed in pairs.

The earliest fossils referred to the Coniferæ are trunks of large trees occurring in Europe and North America, from the Carboniferous to the Permian, and described under the names of *Dadoxylon*, *Araucarioxylon*, or *Pinites*. These stems exhibit the woody structure characteristic of existing Conifers, and Sir J. W. Dawson states that they are found in association with leaves of Permian genera of *Walchieæ* noticed below, and consequently places them in that family. It has, however, been suggested that at least some of these stems belong to the *Cordaiteæ*, although strong reasons have been propounded against the acceptance of this view. Some of the curious ringed cylinders described under the name of *Sternbergia* or *Artisia* are casts of the pith-cavity of *Dadoxylon*. Stems from the coal-measures have been found with a length exceeding 70 feet.

Leaving these doubtful forms we may proceed to the consideration of the five existing families into which the order may be divided. The *Taxineæ*, or Yews and their allies, have their leaves, which are often of considerable width, arranged spirally; the flowers typically dicœcious; and with the ripe seed enclosed in a fleshy envelope. We have already mentioned that *Psygmophyllum* (*Gingkophyllum*) is

placed in this family by Dr Schenk; but exclusive of this form we have several genera allied to the existing *Salisburia* or Gingko-tree of Japan and China, characterised by its fan-like leaves (fig. 1401).

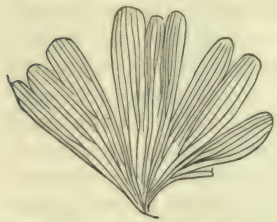


Fig 1401.—Leaf of Gingko-tree (*Salisburia siberica*); from the Lower Cretaceous of Siberia. (After Dawson.)

This genus had an almost world-wide distribution in past times, being abundantly represented from the Permian, and if *Saportea*, from the Carboniferous of Pennsylvania, be rightly included, extending as low as the preceding period. It is very curious, as Sir J. W. Dawson remarks, that this genus should now be restricted to a single Asiatic species, although it will grow in temperate Europe and America, without, however, usually producing fruit. In India it occurs in the Upper Gondwanas. *Rhipidopsis*, from the Lower Jurassic of the Atlas and the Lower Gondwanas of India, is an extinct genus with large leathery leaves usually divided into five wedge-shaped segments, of which the middle one is the largest. Other extinct genera are *Dicranophyllum*, from the Carboniferous of France, China, and Canada; *Trichopitys*, from the Jurassic of Europe; the allied *Czekanowskia*, from the European Rhætic and Jurassic, the Jurassic of China, the Wealden of Portugal, and the Upper Gondwanas of India; and *Fieldenia* and *Phœnicopsis*, the former being from the Miocene of Spitzbergen, and the latter from the Jurassic of Northern Europe and the Upper Gondwanas. Many of these genera have the leaves divided into long slender slips, but in the true Yews the leaves are simply acicular. The existing genus *Taxus*, together with the closely allied or identical *Taxites*, has a wide distribution, being well represented in the Tertiaries and extending down through the Jurassic to the Rhætic. The allied *Cephalotaxus*, of China and Japan, in which the male flowers are in clusters, and the seed is completely enveloped in the fleshy capsule, is represented in the Tertiary and Cretaceous of Greenland; while another existing genus, *Torreya*, occurs in the Tertiaries of Greenland and America. Finally, omitting some less important types, the tropical genus *Podocarpus* occurs abundantly throughout the Tertiaries of the greater part of the world.

The genus *Walchia* (fig. 1402) may be taken as the representative of a group—the *Walchieæ*—which may perhaps serve to connect the Yews with the Araucarias. In the type genus the secondary branches or twigs are arranged alternately in two rows, and carry spirals of angulated acicular leaves; larger leaves covering the primary branches in an imbricating manner. The fruit, according to Dr Schenk, formed true cones, approximating to those of the

Araucarias; but it should be observed that Sir J. W. Dawson considers that their fruit was not in the shape of cones, but was of the type of that of the Yews. This genus occurs in the Permian of Europe and North America. *Ullmania*, of the European Permian and Keuper, is an apparently allied type in which cones are known to have been developed.

In the same family Dr Schenk places the genus *Pagiophyllum* (*Pachyphyllum*), which has thick leathery leaves of triangular form,

Fig. 1402.—Part of branch (*a*) and twig (*b*) of *Walchia piniformis*; from the Permian of Saxony. (After Gutbier.)

arranged spirally on the stem and branches, and uniting at their bases. In Europe it occurs from the Bunter to the Lower Cretaceous; it has also been recorded from the Upper Gondwanas of India, but some of the species from those beds seem to belong to *Araucaria*, to which this genus appears to be nearly related.

The *Araucarieæ* are too well known to require much description; typically they are lofty evergreen trees, with verticillate spreading branches, covered with stiff and flattened leaves, with sharp points, and usually imbricating. The cones are large, globular, and terminal. The existing species are mostly confined to the southern hemisphere, and belong to three genera. Of these, *Dammara*, which extends into the Malay Peninsula, and affords the well-known gum-damar, may be represented in the Upper Cretaceous of Greenland and the United States; but the specimens from the Cretaceous described as *Dammarites* may apparently be cones of Cycads. *Araucaria* itself is now chiefly known from Australia, New Guinea, Norfolk Island, and South America, but in past times had a much wider distribution. Thus it occurs in the Tertiary of the Arctic regions, in the English Eocene, in the Dakota stage of the American Cretaceous, and right through the Wealden and Jurassic of Europe. It also occurs in the Indian Gondwanas, where some of the species have been described as *Araucarites*, while the figured specimen (fig. 1403), which was referred by Dr Feistmantel to

Pagiophyllum, is regarded by Dr Schenk as inseparable from the existing genus. The extinct genus *Cunninghamites* is founded on branches which appear to closely resemble those of the existing *Cunninghamia* of China; it occurs in the Upper Cretaceous and Miocene of the Continent, and the Cretaceous of the United States. Finally, the genus *Albertia*, from the Bunter of Alsace and the Lower Gondwanas of India, may be mentioned here, although it is not certain that its true position is not with the *Abietineæ*.

Fig. 1403. — Branch of *Araucaria* (*Pagiophyllum*) *divaricata*; from the Upper Gondwanas of Cach. (After Feistmantel.)

The family *Taxodineæ* is another ancient type represented from the Permian upwards. The leaves are generally more or less linear, and may be arranged in two rows, or crowded together at the ends of the branches. In *Taxodium* and *Glyptostrobus* the lateral shoots are deciduous. The oldest genus is *Voltzia* (*Glyptolepis*, *Glyptolepidium*), of the Permian and Trias of Europe and the Lower Gondwanas of India; followed by the allied *Leptostrobus*, of the Lower Jurassic of Siberia. *Cyclopitys*, again, from the latter deposits and the Lower Gondwanas of India, is considered to be an ancestral type of the existing *Sciadopitys* of Japan, which connects the typical members of the family with the *Abietineæ*. The genus *Taxodium* is now known by two species from North America, of which *T. distichum* dates from the Upper division of the Laramie beds, and occurs also in the Eocene of Utah, whence it can be traced through the Tertiaries of Alaska, Canada, Greenland, and Spitzbergen, and thus to the Upper Miocene of Œningen in Switzerland. The closely allied *Glyptostrobus* of China, readily characterised by the sculptured scales of the cones and small leaves, has a somewhat analogous distributional history; thus it first appears in the Lower Cretaceous of Greenland, and is also found in the upper part of the same system; thence it extends in one direction through Arctic America to the United States, where it is found in the topmost beds of the Laramie, and in another to Europe, where its range extends from the Lower Miocene (Oligocene) to the Pliocene; *G. europeus* being common to Europe and the Laramie beds. The well-known *Sequoia* (*Wellingtonia*), in which the scales of the cones, instead of imbricating as in the preceding genera, form woody pyramids at right angles to the axis, is now known by two Californian species. Of these *S. sempervirens* has erect leaves arranged in two rows and small round cones; while *S. gigantea*, the "Big tree," has smaller

leaves crowded together, and larger egg-shaped cones. It is remarkable that these two types are represented by allied species in the Lower Cretaceous, where we also find species which are intermediate, and both types continue right through the Tertiaries of Europe and North America, which are connected by the Greenland deposits; while one species has also been found in the Eocene of Australia. Altogether twenty-six species are known.

"This," as Sir J. W. Dawson observes, "is perhaps the most remarkable record in the whole history of vegetation. The Sequoias are the giants of the Conifers—the grandest representatives of the family—and the fact that, after spreading over the whole northern hemisphere and attaining to more than twenty specific forms, their decaying remnant should now be confined to one limited region in America, and to two species, constitutes a sad memento of departed greatness. The small remnant of *S. gigantea* still, however, towers above all competitors as eminently the 'big trees'; but had they and the allied species failed to escape the Tertiary continental submergences and the disasters of the glacial period this grand genus would have been to us an extinct type. In like manner the survival of the single Gingko of Eastern Asia alone enables us to understand that great series of taxine trees with fan-like leaves of which it is now the sole representative."

Geinitzia, from the Upper Cretaceous and Lower Tertiary of both Europe and North America, appears to connect the preceding with the following genus: it has alternating branches, with two rows of small sickle-shaped leaves, between which are scale-like leaves and elongated persistent cones. *Brachyphyllum* is characterised by its extremely short and thick scale-like leaves, which are spirally arranged; it occurs in Europe from the Rhætic to the Wealden, and is also found in the North American Cretaceous. An allied extinct genus is the remarkable *Echinostrobus*, of the Upper Jurassic of Europe and the Indian Upper Gondwanas, in which the stem is flattened, and the branches are covered with imbricating scale-like leaves; while the club-like cones are borne at the summits of short lateral branches. Other extinct genera of this family are *Cyparissidium* from the Rhætic and Upper Cretaceous of Europe; *Inolepis* of the Upper Cretaceous of Greenland; *Chirolepis* from the Rhætic and Lias of France and Switzerland; and *Swedenborgia* from the Rhætic of Palsjö.

The *Cupressineæ*, including the Cypresses, Junipers, and Thujas, are moderate sized or shrub-like trees, usually with very minute scale-like leaves closely adherent to the branches, and generally arranged in two, although sometimes in three or four rows. In some cases, however, the leaves are linear, especially in the young. This family dates from the Upper Trias, and is represented at the present day by some twelve genera. One of the earliest known genera is *Widdringtonites*, from the Keuper of the Continent and the

Jurassic of Europe and the United States; it appears to be in some respects intermediate between other Conifers and the next genus, and its reference to this family is provisional. The existing South African genus *Widdringtonia*, in which the leaves are alternate and crowded, and in the young plant linear, is represented in the Continental Miocene; while *Callitris* from the northern part of the same continent was likewise widely spread over Europe in the Middle Tertiary. In the Upper and Lower Cretaceous of Europe, and also in North America, we meet with the extinct genus *Frenelopsis*; while in the Tertiaries allied forms have been referred to the existing genera *Frenela* and *Actinostrobus*, now confined to the Australian region; *Librocedrus*, which has now a much wider distribution than the latter genera, dates from the higher Cretaceous of Greenland and the United States, and is well represented in the Lower and Upper Miocene of Europe. In *Moriconia* of the Upper Cretaceous of Greenland and Germany, and the Dakota Cretaceous of America, and *Thujites* ranging from the Rhætic[1] to the Upper Jurassic, we have two genera of which the precise affinities are difficult to determine. Of the remaining existing genera known to occur in a fossil state, *Thuja* is found in amber, and has also been recorded from the Upper Cretaceous and Miocene of North America, but these forms are regarded by Dr Schenk as probably referable to *Chamæocypris*. *Biota* of Japan and China, and *Thujopsis* of Japan, occur in the Miocene of Greenland; *Chamæocypris*, of North America and Japan, dates from the Lower Eocene and Miocene of Europe, and probably from the American Cretaceous; *Cupressus* (Cypress), which has a wide distribution in the northern hemisphere, is probably found in amber; while *Juniperus* (Juniper) dates from the Upper Cretaceous of America and Greenland. Finally, *Palæocyparis* which occurs throughout the European Jurassic, and *Phyllostrobus* of the Kimeridgian of France, are allied extinct types. The last family of Conifers is the *Abietineæ*, including the Pines, Spruces, Larches, and Cedars, all of which have tall symmetrical stems, and usually spirally-arranged linear leaves, which may be either flattened or angulated. The cones are usually large and pyriform, with two seeds beneath each scale. We may first mention the extinct genera *Elatides* and *Palissya*, of which the family position is uncertain, since they show some characters of the Pines and others of the Yews. The former occurs in the Jurassic of Siberia, but some of the forms appear to be *Araucarieæ*; while the latter is found in the European Rhætic, the Lower Gondwanas of India, the Australian Newcastle beds, and the reputed Trias of New Zealand. The existing types are usually divided into a number of genera, such as *Pinus* (true Pines), *Abies* (Spruce),

[1] The form from the Carboniferous described under this name is probably a Lepidodendroid.

Larix (Larch), *Cedrus* (Cedar), &c., but the generic determination of many fossil types is extremely difficult, and we can only state here that the group as a whole has undoubtedly existed from the Jurassic, and may not improbably date from the Lias or Rhætic. Finally, the family position of the imperfectly known Rhætic genus *Camptophyllum* cannot at present be determined.

Order 3. Gnetaceæ.—This small order, represented by the genera *Ephedra*, *Gnetum*, and *Welwitschia*, is not certainly known to be represented in a fossil state, although several forms have been referred to the first-named genus.

CHAPTER LXVIII.

SERIES PHANEROGAMÆ—continued.

Class Angiospermæ.

Class II. Angiospermæ.—With this class we come to the highest development of plant life, characterised by the complete enclosure of the ovules and seeds in the ovary, and by the more or less rudimental condition of the endosperm. As they are highest in point of development, so these plants are characteristic, as a whole, of the latter periods of the earth's history, so that the Tertiary and recent periods are well described as the "age of Angiosperms." The class may be divided into the two great subclasses of Monocotyledons and Dicotyledons, of which the former is the more generalised, and the first to make its appearance in time.

Subclass I. Monocotylæ.—The Monocotyledons are plants having only a single seed-leaf or *cotyledon;* and with an endogenous, or inwardly growing stem, in which there are consequently no annual rings of growth. It includes the Palms, Grasses, Lilies, &c.; and it appears that the Palms and Grasses are the earliest known forms; the perianthed types, or those with large and conspicuous flowers, not making their appearance till a later date.

There is indeed some doubt as to the earliest appearance of the subclass, but it appears to be certain that most of the Palæozoic forms which have been described as Monocotyledons are referable to Gymnosperms. There occur, however, certain forms of doubtful affinity in the Upper Palæozoic, which have been termed "pro-Angiosperms," or types imperfectly developed from a Pteridophytic or Gymnospermic stock, which we may proceed to notice. The best known is the genus *Spirangium*, ranging from the Carboniferous to the Wealden; this is based on certain spindle-like bodies, which are believed to consist of from five to ten linear valves enclosing a central cavity, the valves being in some cases spirally twisted. Their affinities are at present totally obscure. From the Russian Permian

a leaf with a net-like venation described under the name of *Dichoneuron*, has been regarded as a Monocotyledon, but apparently on quite insufficient grounds. The genus *Œthophallum*, from the Trias of the Vosges, which has linear leaves arranged in groups of three on the branches of a woody stem, and long seed-bearing spikes, has also been referred to this subclass. Certain fruit-spikes from the same deposits described as *Echinostachys* may belong to kindred types. Again, the long ribbon-like leaves found in the Rhætic and Jurassic and known as *Yuccites*, have been looked upon as indicating plants allied to the existing *Dracæna;* but it is quite possible that remains of totally distinct types of vegetation have been included under this name. In the Upper Trias and Lias of Switzerland occurs the imperfectly known *Bambusium*, which Mr J. S. Gardner regards as an undoubted Monocotyledon, although Dr Schenk suggests affinity with the Equisetaceæ. The former writer also regards as Monocotyledonous a stem from the Yorkshire Oolites described as a Calamite. Plants from the Jurassic which have been named *Naiadita*, *Bensonia*, &c., are not Phanerogams at all; while *Aröides* of the Great Oolite is based on a Crinoid. Stems with a rush or grass-like form from the Purbeck appear, however, to be true Monocotyledons. Finally, *Rhizocaulon*, from the Upper Eocene of the Paris basin, is based on the evidence of a stem which may indicate a plant allied to the *Cyperaceæ*.

Leaving these doubtful types, we may proceed to the consideration of Monocotyledons which can be systematically placed.

Order 1. Liliifloræ.—This order includes the Lilies, Irises, Yuccas, and their allies, most of which have conspicuous perianthed flowers, which vary considerably in structure, and may be of large size. The plants may be perennial, but are more usually annual, with rhizomes or bulbs. The *Liliaceæ* (Lilies, Tulips, Aloes, Yuccas, &c.) are but of little palæontological importance. From the Eocene and higher Tertiaries plants have been described under the names of *Agavites*, *Yucca*, and *Dracæna*, the two last being existing genera; but Dr Schenk considers that most of these belong to *Dracæna* (Dragon-tree), now found in the Canaries, Africa, and India. Plants of the genus *Smilax*—the type of a subfamily of *Liliaceæ*—occur in the European Tertiaries from the Eocene upwards; although it seems doubtful if forms described as *Smilacina* and *Majanthemophyllum* really belong to this group. The *Juncaceæ*, or Rush family, are known by species of *Juncus* from the Upper Miocene of Œningen; and, according to Dr Schenk, a species of *Iris* from the same deposits is the only fossil representative of the *Iridaceæ*, although several other fossils have been described under that name. In the *Dioscoreaceæ* (Yams), *Dioscorites*, from the European Miocene, is probably allied to *Dioscorea;* while in the Pine-apple family, or

Bromeliaceæ, the typical *Bromelia* apparently occurs in the same deposits. Other fossils referred to these families are, however, distinct.

Order 2. Enantioblastæ.—There is some uncertainty as to whether this small order is represented in a fossil condition, but it is not improbable that *Eriocaulon* occurs in the Tertiary of the United States.

Order 3. Spadicifloræ.—With this order, which comprises the Palms, Screw-pines, and Arums, we come to one of considerable palæontological importance, as including several of the earliest representatives of the class. They are typically tall plants, with large wide-spreading leaves, and the inflorescence forming a spadix, generally enveloped in a large spathe, and without a petalled perianth; the seed being generally large, and often of huge size. The first family of the *Palmaceæ* now includes about one thousand species from the warmer regions of the globe, and dates back to the Upper Cretaceous. In the higher Cretaceous of Europe we meet with Palms referred to the extinct genus *Flabellaria*, which also ranges into the Miocene, and has been recorded from the Cretaceous of the United States. *Fasciculites*, from the Cretaceous of Greenland, is regarded

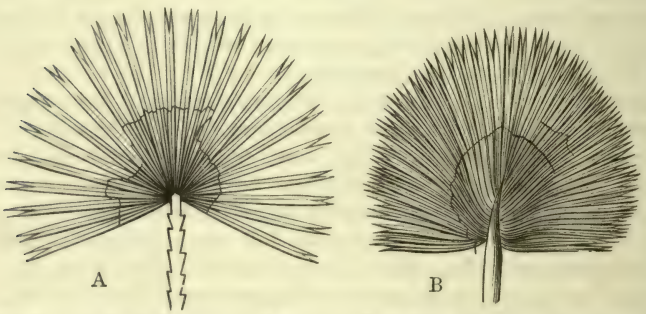


Fig. 1404.—A, Leaf of *Chamærops helvetica*; from the Upper Miocene of Switzerland. B, Leaf of *Sabal major*; from the Lower Miocene of France. Reduced.

with some hesitation as a Palm-stem; and Mr Gardner figures Palm-wood from the Folkestone Gault; but many other earlier fossils, such as *Palæospathe*, are not Palms at all. In the Tertiary Palms are abundant, and from the Eocene to the Upper Miocene we meet with forms with pinnate leaves allied to the existing *Phœnix* (Date-palm), which have been described under that name, or as *Phœnicites* and *Calamopsis*. Of the group with fan-like leaves we have already mentioned *Flabellaria*, and throughout the European Tertiary there occur leaves referred to the Old World genus *Chamærops* and to *Sabal* of North America (fig. 1404); both of which genera have a more northerly distribution than any other types. *Sabal*

major (fig. 1404) occurs in the Lower and Middle Miocene of Europe, and also in the Miocene of Northern India; while remains of the same genus have been described from the Tertiary of the United States. In the Lower Eocene of Europe and the Chalk of Fuveau large fruits occur known as *Nipadites* (fig. 1405), from their resemblance to the triangular fruits of the Oriental and Australasian genus *Nipa*, which some writers class with the Palms and others with the *Pandanaceæ*. There is considerable doubt whether the small family *Cyclanthaceæ*, of tropical America, is represented in a fossil state, but fragmentary leaves from the Lower Eocene of Sézanne have been described as *Ludoviopsis*, from their supposed resemblance to those of *Ludovica*. The well-known *Pandanaceæ*, or Screw-pines, are trees or shrubs with long simple imbricated leaves, usually spined on the edges and back, and unisexual or polygamous flowers, without perianth, and covering the whole of the spadix; the fruit being in the form of drupes with single seeds, or berries with numerous seeds. All the living forms are tropical. Leaves from the Tertiary and Upper Cretaceous of Europe have been referred to *Pandanus;* but it is a question whether at least some of these do not indicate a distinct genus. In the Cretaceous and Jurassic of Europe, extending as far north as Greenland, there occur fruits to which the name *Kaidacarpum*[1] has been applied, and which are regarded by their describer, Mr Carruthers, as undoubtedly Pandanaceous, although Dr Schenk is not absolutely satisfied of the correctness of this reference. The fruit consists of a thick spadix, with bunches of drupes, each of which contains a single seed; the whole arrangement being strikingly like that of the existing *Sussea*. *Podocarya* is an apparently allied fruit from the Inferior Oolite; and some authorities regard *Williamsonia* (p. 1528) as related to this genus. *Goniolina*, from the Kimeridgian and Corallian of France, is founded on compound fruits which are compared by Mr Gardner to those of *Pandanus*, and of which the description is as follows:—

Fig. 1405.—Fruit of *Nipadites ellipticus;* from the London Clay. Reduced.

"Small ovoid aggregated fruits, like those of *Pandanus*, borne on a naked, cylindrical, and relatively slender petiole. The heads of the very numerous fruits are arranged in spirals and regular, pressed together, and barely a millimetre across. They are of hexagonal shape, and six keels extend from the angles and meet in a raised point at the centre. The interior axis is cylindrical, and impressed by scars made by the bases of the fruits, completing its likeness to *Pandanus*."

[1] Correctly *Cædacarpum*.

The reed-like plants of the family *Typhaceæ* occur throughout the Tertiary, where we have *Typha* (Reed-mace) or the allied *Typhæoloipum*, and *Sparganium*, although it is doubtful if the Cretaceous plants referred to these genera are rightly named. The *Araceæ* (Arums and their allies) appear to date from the Upper Cretaceous, although it is extremely uncertain if the Tertiary plants described as *Aröites* and *Aronites* really belong to this family. *Acorus* (Sweet-flag) occurs in the Miocene of Spitzbergen, and is also found in amber; and *Pistia*, a tropical water-weed allied to the common

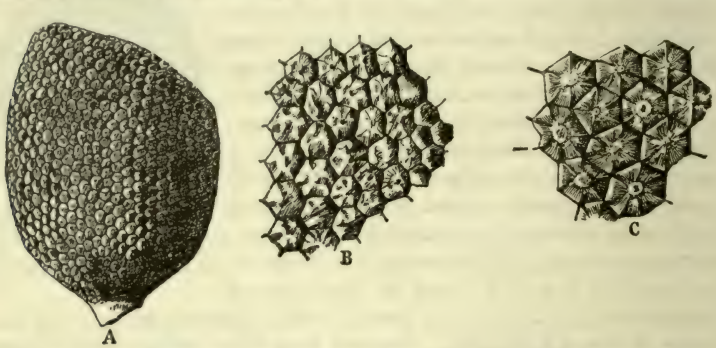


Fig. 1406.—A, Fruiting-organ of *Goniolina*; B and C, The individual fruits enlarged; from the Kimeridge Clay of France. (After Saporta and Marion.)

Duck-weed (*Lemna*), occurs in the Laramie beds of America and the Upper Cretaceous of the Continent; but the plants from the Westphalian Chalk and the Laramie beds, described as *Pistites* and *Lemnophyllum*, according to Dr Schenk, are not Monocotyledons. *Lemna* has been described from the Laramie and Middle Tertiary of North America, and also from the Miocene of Würtemberg. *Pothocites*, of the Carboniferous, which has been referred to this family, is part of a Sigillarian. In the aquatic *Naiadaceæ* we have remains of the fluviatile genera *Posidonia* and the marine *Zostera* (*Zosterites*) dating from the Upper Cretaceous of both the eastern and western hemispheres. *Cymodocea* may also date back to the Eocene, although many of the forms described under its synonym of *Caulinites* are totally different. *Naias* occurs certainly in the Miocene of Œningen, and perhaps in lower beds; while *Potamogeton* (Pond-weed), with its dimorphic leaves, dates from the Upper Eocene of Aix, and is also found in the Tertiaries of North America.

Order 4. Glumifloræ. — This order includes the Grasses, Sedges, &c., and is of but little importance to the palæontologist. In the *Gramineæ*, exclusive of some very doubtful forms, we may notice that *Bambusa* (Bamboo) occurs in the Pliocene of Europe;

but that the so-called *Bambusium* is probably Equisetaceous. *Arundo* and the allied *Phragmites* are stated to make their first appearance in the Upper Cretaceous of both hemispheres; while *Pseudophragmites* and *Arundites*, dating from the Eocene, are more or less closely allied extinct types. In the *Cyperaceæ* (Sedges) numerous fossil Tertiary plants have been described as *Carex*, *Cyperus*, *Cyperites*, and *Scirpus*, the former being also recorded from the Laramie; but all these determinations are exceedingly doubtful, and it can only be stated with certainty that *Cyperus* occurs in the Œningen Miocene.

Order 5. Scitamineæ.—The past history of this large tropical order is even more imperfect than that of the last. In the *Musaceæ* (Plantain) large leaves, from the Eocene and higher Tertiaries, have been described under the names of *Musaphyllum* or *Musa*, but Dr Schenk suggests that some at least of these may belong to the *Araceæ*. Under the name of *Zingiberites* imperfect leaves, from the Upper Cretaceous of Greenland and the Swiss Tertiary, have been regarded as indicating fossil *Zingiberaceæ;* and a similar position has been given to *Amomocarpum* and *Amomophyllum* of the Upper Eocene of Paris. Finally, *Cannophyllites*, of the latter beds, has been considered as an ally of the existing *Canna* among the *Marantaceæ*.

Order 6. Gynandræ.—The only fossils hitherto referred to the Orchids are the *Protorchis* and *Palæorchis*, of the Middle Eocene of Monte Bolca; and it is probable that the greater number of these plants, with their highly specialised and complexly perianthed flowers, are of comparatively recent origin.

Order 7. Helobiæ.—The last order comprises aquatic and marsh plants which date back to the Upper Cretaceous. *Laharpia*, from the Miocene of Œningen, may perhaps indicate a member of the *Jungaginaceæ* allied to the existing *Scheuchzeria*. In the *Alismaceæ* some of the forms, occurring from the Cretaceous upwards, referred to *Alisma* and *Sagittaria*, may be correctly named. *Butomus* has been recorded from the Miocene of Œningen. Of the *Hydrocharitaceæ*, *Stratiotes* and *Hydrocharis* have been described from Œningen, and the extinct *Hydrocharites* from the Miocene of Bonn; while *Valisneria* and *Ottelia* date from the Upper Eocene of the Paris basin in Europe, but the former also occurs in the Laramie of America, and thus carries back its origin to the Cretaceous.

Subclass II. Dicotylæ.—The Dicotyledons are plants having two cotyledons or seed-leaves, and the stems exogenous like those of the Gymnosperms. They represent the highest type of plant-life, their organisation being a great step in advance of the Monocotyledons. The earliest known members of this group occur in the reputed Lower Cretaceous of Greenland, where, however, only a

few forms are known; but when we come to the Dakota stage of the United States, which is usually correlated with the lower part of the Upper Cretaceous of Europe, Dicotyledons formed a large proportion of the flora, more than three hundred species having been described in 1885, which belong to both sections of the subclass. This abundance of forms pointing to the conclusion that the origin of Dicotyledons must be looked for in considerably earlier epochs.

Very different views are held by authorities as to the classification of Dicotyledons, some dividing them into several primary groups, while others only admit the three divisions Apetalæ, Polypetalæ, and Gamopetalæ. Dr Endlicher, however, makes only two divisions—Choripetalæ and Sympetalæ,—and since this arrangement is adopted by Dr Schenk in his 'Palæophytologie,' it will be followed in this work.

The larger proportion of the Cretaceous and Eocene Dicotyledons belong to the Choripetalæ, and especially to those orders in which the flowers are fertilised merely by the agency of the wind; the more specialised Sympetalæ, which require the aid of insects for this purpose being in great part of later date. The labours of Baron von Ettingshausen have shown that the Cretaceous and early Tertiary Dicotyledonous (and also the Monocotyledonous and Gymnospermous) flora was almost similar throughout the world; and that its present division into provinces is in great part due to the influence of one or more glacial periods. Bearing in mind this world-wide distribution of so many of the genera, it will be unnecessary in most cases to do more than mention their earliest established occurrence; and owing to the immense number of families only the more important types can be even mentioned at all. Space will not permit any reference to the gradual differentiation of the existing floras, or to the interesting distribution of modern arctic types in the Pleistocene, for which the reader must refer to the works of Baron von Ettingshausen, Sir J. W. Dawson, and other writers. It should be mentioned that in the case of trees known only by the leaves the generic determination may be open to doubt in some cases.

Division A. Choripetalæ.—This large group is characterised by the petals being either absent, or if present not united together.

Order 1. Amentaceæ.—This order comprises trees which are typically apetalous with the male flowers in the form of catkins. It includes five families, and comprises some of the earliest known representatives of the subclass. The first family, *Casuarinidæ*, is now represented only by the well-known *Casuarina* of the Australian and the eastern Malayan regions: this genus apparently occurs in the Lower Tertiary of Sumatra, but it is very improbable that the Euro-

pean fossils described under this name are really referable to the group. With the *Cupuliferæ*, containing the Alders, Birches, Hazels, Beeches, Oaks, &c., we come to a large group well represented in a fossil state, many of the forms being known by the seeds as well as the leaves. The existing genera *Alnus* (Alder), and *Betula* (Birch), are recorded from the Laramie and Dakota stages of the Upper

Fig. 1407.—Leaf of *Alnus gracilis;* from the Miocene of Europe. (After Unger.)

Fig. 1408.—Leaf of *Betula cuspidens*, and fruit of *B. dryadum;* from the Lower Miocene of Europe. Reduced. (After Saporta and Brongniart.)

Cretaceous of the United States, and likewise from the Cretaceous of Greenland, but Dr Schenk suggests some doubt as to whether these forms really belong to the living genera, and would prefer to call them *Alnophyllum* and *Betulophyllum*. An allied Cretaceous form has been named *Alnites*. In the Tertiary the existing genera (figs. 1407, 1408) are well represented from the Eocene upwards. In the next subgroup *Corylus* (Hazel), *Ostrya*, and *Carpinus* (Horn-

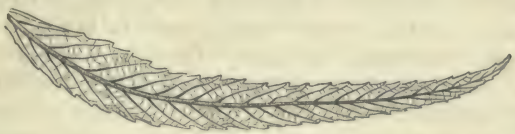


Fig. 1409.—Leaf of *Dryophyllum;* from the Lower Eocene of Europe. Reduced. (After Saporta.)

beam) also occur from the Eocene, while the former is recorded from the Laramie. *Fagus* (Beech) dates from the Dakota stage, which has also yielded remains referred to *Castanea* (Chestnut); and *Castanopsis* has been recorded from the American Eocene, and the Australian Tertiary, although it is suggested that some of the forms so named may belong to *Dryophyllum*. The latter name is applied

to elongated leaves (fig. 1409), from the Upper Cretaceous and Eocene of both Europe and North America, which appear to be in some respects intermediate between those of *Castanopsis* and the earlier species of Oaks. The leaves of *Quercus* (Oak) are subject to an enormous amount of variation, rendering the determination of fossil forms a work of extraordinary difficulty. One of the most ordinary and characteristic types of leaf is shown in fig. 1410, but in the early Tertiary and Upper Cretaceous we meet with long slender oak-leaves approximating to those of *Castanea* in general contour. The earliest recorded occurrence of the genus is in the Dakota stage, and it is abundantly represented throughout the Tertiaries; leaves, from the Tertiary of Australia, in which country oaks are now absent, have been described as *Quercus*, but doubt has been thrown on this determination. In the *Juglandaceæ*, the genus *Juglans* (Walnut) probably dates from the Upper Cretaceous of America and Greenland; the Tertiary species of which a leaf is figured in the woodcut occurs on both sides of the Atlantic, and appears to be closely allied to the existing *J. regia*. The name *Juglandites* has been applied to leaves from the Upper Cretaceous and Eocene of Europe, which are believed to indicate an allied type. *Carya* (Hickory), now confined to America, is recorded from the Cretaceous of that country, and occurs in both the European and American Tertiaries. Similarly the Old World *Pterocarya* is represented in the Tertiaries of both hemispheres, while the Oriental genus *Engelhardtia* occurs in the Upper Eocene of Aix, where it has been described as *Palæocarya*. In the *Myricaceæ* the single genus *Myrica* makes its first appearance in the Upper Cretaceous of Greenland and North America, and is common in the Tertiaries. Of more palæontological importance is the family *Salicaceæ*, in which both *Populus* (Poplar) and *Salix* (Willow), (fig. 1415, *d*), date from the Upper Cretaceous. A leaf from beds at Komi in Greenland, which have been regarded as Lower Cretaceous, has, indeed, been described as *Populus*, but according to Mr J. S. Gardner on totally insufficient grounds; but Sir J. W. Dawson considers that *Salix*

Fig. 1410.—Leaf of *Quercus conferta*. Recent. Reduced. (After Schenk.)

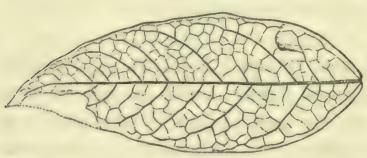


Fig. 1411.—Leaf of *Juglans acuminata*; from the Miocene of Europe. Reduced. (After Schenk.)

may occur in the Lower Cretaceous of the United States. The species of *Populus* of which a leaf is figured in the woodcut extends from the Lower Miocene to the Pliocene.

Fig. 1412.—Leaf of *Populus latior*: from the Miocene of Europe. Reduced. (After Schenk.)

Order 2. Urticinæ.—This order contains the three families *Ulmaceæ*, *Urticaceæ*, and *Ceratophyleæ*; the last of which requires no further mention. In the first family *Ulmus* (Elm) makes its first undoubted appearance in the Upper Eocene (Lower Oligocene) of Aix, in Provence, but the Asiatic and American *Planera* dates from the Laramie Cretaceous, and is common in the European Tertiary. *Celtis* (Nettle-tree), now abundant in southern Europe, is well represented throughout the Continental Miocene; while *Morus* (Mulberry) is unknown before the Upper Miocene. The tropical *Artocarpus* (Bread-fruit) dates from the Upper Cretaceous of Greenland, and also occurs in the Œningen Miocene; and it is probable that some of the forms from the Lower Eocene and Miocene of Europe described under the names *Artiocarpidium* and *Artiocarpoides* are allied types, although others belong to *Ficus*. The latter genus includes the numerous species of Fig mostly characteristic of the warmer regions; it dates from the Greenland Cretaceous and the Laramie, and is abundant in the Tertiaries of many parts of the globe. The names *Ficonium* and *Protoficus* have been applied to fig-like leaves from the Eocene, some of which may belong to this family. In the *Urticaceæ* it has been considered that *Urtica* (Nettle) occurs in the Middle Miocene of Styria, but this requires confirmation. That the family occurred in the Tertiary is, however, proved by the genus *Forskohleanthemum*, which is found in amber, and is allied to the existing tropical and subtropical genus *Forskohlea*. Here may be mentioned certain genera of uncertain affinity which are considered by Dr Schenk to be allied to the *Urticaceæ*, although Sir J. W. Dawson would place them near the *Platanaceæ*; these comprise the Upper Cretaceous *Credneria* and *Ettingshausia* from Europe; *Macclintockia*, with more elongated leaves, from both the Cretaceous and Eocene; and *Protophyllum* of the American Cretaceous, which is considered by Dr Schenk to be allied to the existing Urticaceous genus *Laportea*.

Order 3. Piperineæ.—In this group *Piper* (Pepper) and allied forms described as *Piperites* occur in the Lower Tertiary of Java and Sumatra; the existing forms being now tropical.

Order 4. Centrospermæ.—This large order, which includes the

Pinks and Portulacas, is very sparingly represented in a fossil state, but we may mention that *Polygonum*, *Coccolabis*, and *Salsola* occur in the European Miocene; while *Pisonia* is found in the Middle Tertiaries of both Europe and North America.

Order 5. Polycarpieæ.—Of the nine families constituting this order only the *Lauraceæ*, *Nymphæaceæ*, and *Magnoliaceæ* are of much importance to the palæontologist. In the *Lauraceæ* the existing genera *Laurus* (Laurel), *Sassafras* (fig. 1415, *a*) *Cinnamomum* (Cinnamon, fig. 1413), *Persea* (Alligator-pear, fig. 1414), and *Oreodaphne*, occur in the Upper Cretaceous of Europe or the United States, and throughout the greater part of the Tertiaries. With the exception of *Laurus* all these genera are now tropical or subtropical, *Persea* and *Oreodaphne* being restricted to America; and their abundance in the European Tertiaries affords conclusive proof of the warm climate of that epoch. *Cinnamomum* also occurs in the Tertiary of Australia, and *Litsæa* in that of Borneo. In the *Berberidaceæ* the type genus *Berberis* (Berberry) dates from the Lower Miocene; but with the *Menispermaceæ* we return to a family dating from the Cretaceous, where it is represented in the United States by the extinct *Menispermites*. *Cocculus*, of the Oriental region, is found in the European Pliocene, and has also been recorded from the Eocene, but the latter determination is doubtful. Leaving out some other unimportant types we may pass to the family *Magnoliaceæ*, which has a palæontological history of

Fig. 1413.—*Cinnamomum polymorphum*. *a*, Leaf; *b*, Flower; from the Upper Miocene of Europe. Reduced.

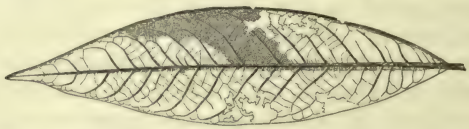


Fig. 1414.—Leaf of *Persea princeps*; from the Upper Miocene of Switzerland. Reduced. (After Heer.)

considerable interest. The type genus *Magnolia*, so well known for its magnificent white flowers, is now confined to Asia and North America, but in the Tertiary was spread over all Europe, and has also been recorded from Australia; its earliest appearance being in the Upper Cretaceous of France and the United States. The other well-known genus is *Liriodendron*, now represented only by the handsome Tulip-tree (*L. tulipifera*) of eastern America, but in former times having a wide distribution, and dating from the Cretaceous of

both hemispheres. The leaves (fig. 1415, *b*) are readily recognised by their lyre-like form and deep terminal emargination.

The observations of Dr Newberry on this genus are so interesting that, with some omissions and verbal alterations, they may be quoted at length. The doctor observes, "that a plant so splendid should stand alone in the vegetation of the present day excited the wonder of the earlier botanists, but the Sassafras, Sweet-gum, and the Sequoias of the West afford similar examples of isolation. Three species of *Liriodendron* occur in the Cretaceous of New Jersey, and others have been obtained from the Dakota group in the West, and from the Upper Cretaceous of

Fig. 1415. — Leaves of American Cretaceous Dicotyledons. *a*, *Sassafras cretaceum*; *b*, *Liriodendron Meeki*; *c*, *Leguminosites Marcouanus*; *d*, *Salix Meeki*. (After Dana and Lesquereux.)

Greenland. Though differing considerably among themselves in size and form, all these have the deep sinus of the upper extremity of the leaves so characteristic of the genus, and the venation is also essentially the same. Hence we must conclude that the genus, now represented by a single species, was in the Cretaceous age much more largely developed, having many species, and those scattered over many lands. In the Tertiary the genus continued to exist, but the species seem to have been reduced to one, which is hardly to be distinguished from that now living. In many parts of Europe leaves of the tulip-tree have been found, and it extended as far south as Italy. Three European species have, indeed,

been described, but they are all so like the living form that they should probably be united with it. We here have a striking illustration of the wide distribution of a species which has retained its characters both of fruit and leaf quite unchanged through long migrations and an enormous lapse of time. In Europe the tulip-tree, like many of its American associates, seems to have been destroyed by the cold of the glacial period, the Mediterranean cutting off its retreat; but in America it migrated southward, and returned northward with the amelioration of the climate."

The mainly tropical family of the *Anonaceæ* includes trees and shrubs closely allied to the Magnolias, and the existing American and Malayan genus *Anona* is represented in the Upper Cretaceous and Tertiary of the United States, while in Europe it is found from the Eocene to the Pliocene. The extra-tropical North American genus *Asimina* occurs in the Laramie and Eocene of the same regions. The large family of the *Ranunculaceæ* is sparingly represented in a fossil state; thus *Clematis* has been recorded from the reputed Pliocene of Japan, the Miocene of Œningen, and the Eocene of Croatia, but it is not absolutely certain that the determination is correct. The same remark applies to other Tertiary plants referred to *Ranunculus* and *Helleborus* (*Helleborites*). The names *Dewalquea* and *Debea* have been applied to Upper Cretaceous plants considered to belong to this family, although Dr Schenk suggests affinity with the *Aroideæ*. The Water-lilies of the family *Nymphæaceæ* date from the Upper Cretaceous, where we meet with remains of the existing genus *Nelumbium*, succeeded in the Upper Eocene (Oligocene) by *Nymphæa* (fig. 1416). Seeds from the Miocene of Germany, described as *Holopleura*, are considered to be allied to those of the celebrated *Victoria*, of the African lakes. Other Tertiary types have been referred to extinct genera under the names of *Anœctomeria*, *Nymphæites*, and *Carpolithes*. Finally, the genus *Nuphar* is unknown before the Norfolk Forest-bed, where we meet with the existing Yellow Water-lily.

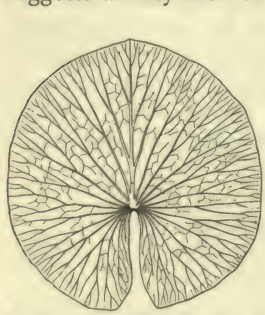


Fig. 1416.—Under surface of a leaf of *Nelumbium Dumasi*; from the Upper Eocene of France. One-eighth natural size. (After Saporta.)

Order 6. Rhoëdinæ.—Of the *Papaveraceæ* (Poppies) and *Cruciferæ*, constituting this order, the palæontological history is almost a blank, although a few Miocene forms have been referred to them. The *Cruciferæ* include the Cabbage tribe.

Order 7. Cistifloræ.—This order is of somewhat more palæontological importance. In the *Violaceæ* (Violets and Pansies), *Anchietea* is recorded from the Miocene of Auvergne; while in the

Cistaceæ (Rock-roses) a *Cistus* has been described from that of Germany. A *Kiggelaria*, from the Upper Eocene of Saxony, is the only fossil representative of the *Bixaceæ*. The tropical family *Ternstrœmiaceæ* is somewhat better known; thus we find *Pentaphylax* in amber of middle Tertiary age, while *Stuartia* also occurs in amber as well as in Pliocene beds. The genera *Ternstrœmia*, *Freziera*, and *Sauruja* are known as fossils only by their leaves; the first dating from the Cretaceous of Bohemia, the second from the Eocene, and the third from the Miocene. Another tropical family, the *Dipterocarpeæ*, is represented in the Eocene of Sumatra and Borneo by species of the genus *Dipterocarpus*, now inhabiting the same regions, and yielding the balsam of Copaiba.

Order 8. Columniferæ.—This order includes the four families *Tiliaceæ*, *Sterculiaceæ*, *Malvaceæ*, and *Bombaceæ*. In the first the existing genera *Tilia* (Lime), *Grewia*, and *Elæocarpus* occur fossil, the former dating from the Laramie, and the two latter from the Upper Eocene or Lower Miocene. Of extinct genera we may mention the Cretaceous and Lower Eocene *Grewiopsis* and *Apeibopsis*; the former being known by leaves, and the latter by gourd-like fruits, of very common occurrence in the London Clay, which resemble those of the existing American genus *Apeiba*. *Nordenskiœldia* is based on allied fruits from the Tertiary of Spitzbergen. The *Sterculiaceæ* is an exclusively tropical family of trees and shrubs, in which the existing genus *Sterculia* commences in the Dakota Cretaceous, and continues right through the European Tertiaries. Extinct genera are *Dombeyopsis*, *Pterospermites*, and *Fracastella*, all of which commence in the Cretaceous, and continue to the Lower or Middle Tertiary. The leaves of *Dombeyopsis* (fig. 1417) are acutely trilobate, with numerous veins. The *Malvaceæ* and *Bombaceæ* have left but little record of their past history; but *Bombax* occurs in the Upper Eocene of Europe.

Fig. 1417.—Under surface of a leaf of *Dombeyopsis Deckeni*; from the Lower Miocene of Germany. One-fourth natural size. (After Schenk.)

Order 9. Gruinales.—The palæontology of this order, which includes Geraniums, Tropæolums, Sorels, Flax, and Balsams, may be summed up in very few words. It is thought that *Geranium* may occur in amber; the Tertiary *Oxalidites* is referred to the *Oxalidaceæ*; but the Tertiary fruit described

as *Linum* (flax) is of very doubtful value as evidence of the family *Linaceæ*.

Order 10. Terebinthinæ.—Of the families constituting this order, several are very imperfectly known before the present epoch. In the *Rutaceæ* (Rue-worts) the genus *Xanthoxylon*, which is now mainly tropical, occurs in the Upper Eocene and Lower Miocene of Europe, and also in the North American Tertiaries. *Ptelea* appears at the same date, but persists to the close of the Miocene period. With regard to *Protamyris*, from the Tertiary of Croatia, which was described as being allied to the existing *Amyris*, there is considerable doubt whether it really belongs to this family at all. In the *Simarubaceæ* the Indian and Chinese genus *Ailanthus* was formerly more widely spread, being found in Europe from the Upper Eocene to the Upper Miocene. There is some doubt whether the plants from the Middle Eocene of Monte Bolca, referred to the genus *Guajacites*, are really representatives of the American family *Zygophyllaceæ*. The large family of the *Anacardiaceæ*, typically represented by the tropical *Anacardium* (Cashew-tree), is known by a considerable number of fossil forms, although there is some doubt as to whether several of these are rightly determined. From the Upper Eocene of Provence a fruit has been referred to this family under the name of *Trilobium*. *Pistachia* (Pistachio), now distributed over the temperate zone of the northern hemisphere, is known from the European Upper Eocene and Miocene; while the name *Anacardites* has been given to leaves occurring from the Cretaceous to the Miocene. A large number of species, dating from the Upper Cretaceous and continuing through the Tertiaries of both Europe and America, have been referred to *Rhus* (Sumach), but it is probable that some of these belong to other plants. Of the other families, it will suffice to say that in the *Coriariaceæ* the genus *Coriaria* occurs from the Lower Miocene to the Pliocene of Europe.

Order 11. Æsculinæ.—In this order the family *Sapindaceæ*, with the exception of *Kœlreuteria*, *Staphylea*, and *Æsculus*, is now confined to the tropics, and includes trees of large size. Fruits from the London Clay termed *Cupanoides*, and others from the Miocene of Croatia described as *Cupanites*, are believed to have belonged to sapindaceous trees allied to *Cupania*. *Paullinia* has been recorded from the Middle Tertiaries of the Continent, while *Kœlreuteria* occurs in the Upper Miocene. Fruits from the Tertiary of Eubæa have been referred to *Nephelium*, while an imperfect leaf from Borneo probably belongs to the same genus. *Sapindus*, which in America does not range north of Texas, is abundantly represented in the Upper Cretaceous and Tertiaries of both the Old and New Worlds. *Æsculus* (Horse-chestnut) has been recorded from the Laramie beds, but in Europe appears to be unknown

before the Lower Miocene, although said to be abundant in the earlier Tertiaries of Japan. *Dodonæa*, now mainly confined to the southern hemispheres, is found in the Tertiaries of Europe and North America. Again, *Staphylea*, which is unknown as a fossil in Europe, is abundant in the Eocene of the United States. The genus *Acer* (Maple and Sycamore), now widely distributed, is represented by a great number of fossil species ranging from the Laramie stage upwards. The leaves are subject to great variation in form, the most remarkable types occurring in the Pliocene *A. polymorpha;* the woodcut shows a leaf of the more ordinary form together with one of the characteristic winged seeds.

Fig. 1418.—Leaf and seed of *Acer acutilobata;* from the Miocene of Germany. One-third natural size. (After Schenk.)

The mainly tropical family *Malpighiaceæ* is represented in the Tertiary from the Upper Eocene to the higher Miocene by several existing genera, such as *Stigmaphyllum*, *Banisteria*, *Tetrapteris*, and *Hiræa*, together with the extinct *Malpighiastrum*, ranging from the Eocene to the Upper Miocene or Pliocene; the whole of the above-mentioned existing genera being now confined to America.

In this place we may mention the family *Platanaceæ* which is placed by some writers in the Amentaceæ or Urticinæ, but of which the ovary and the general appearance of the trees bring it near to the Maples and Sycamores. Of the single genus *Platanus* (fig. 1419) there is now one species in Asia Minor and another in North America; fossil forms occurring as low down as the Dakota Cretaceous and continuing through the Tertiaries of both hemispheres, their last appearance in Europe being in the Œningen Miocene.

Fig. 1419.—*Platanus aceroides*. *a*, Leaf; *b*, The core of a bundle of pericarps; *c*, A single fruit or pericarp, natural size. Upper Miocene.

Order 12. Frangulinæ.—Among the more important fossil forms found in this order we may mention that in the *Celastraceæ* *Euonomus* (Spindle-wood) makes its first known appearance in the Miocene by forms allied to Indian types; while *Celastrus* dates from the Cretaceous of Greenland, and is known by a host of Tertiary species. The two extinct genera *Celastrophyllum* and *Celastrinites* commence in the Upper Cretaceous, the one continuing to the Pliocene but the other unknown above the Eocene. Finally, remains from the Miocene of Styria have been referred to the South American

genus *Maytenus*. Whether the *Hippocrateaceæ* and *Pittosporeaceæ* occur fossil is uncertain, although Tertiary plants from Styria have been referred to *Hippocratea* and others from Provence to *Pittosporum*.

In the *Aquifoliaceæ* the genus *Ilex*, typically represented by the Holly, is abundantly represented throughout the Tertiaries, and is also recorded from the Cretaceous of both hemispheres, commencing in the Dakota stage. The extensive family of the *Rhamnaceæ* has afforded ample proof of its existence in earlier periods; thus the Old World genus *Paliurus*, and the tropical *Zizyphus* (Jujube) both date from the Cretaceous and persist in Europe till the Pliocene. In the Laramie Cretaceous and the European Tertiary we have the existing American genus *Berchemia;* while other plants from the Laramie have been made the types of an extinct genus *Rhamnites*. Finally, the genus *Rhamnus* (Buckthorn), mainly characteristic of the northern temperate zone, can be traced back to the Upper Cretaceous of the Old and New Worlds. The last family of this order is the *Vitaceæ*, in which we find *Cissus*, of the tropics, recorded from the Miocene of Croatia and elsewhere; allied Cretaceous forms described as *Cissites* and *Chondrophyllum;* while *Vitis* (Vine) itself is known to date as far back as the Laramie Cretaceous.

Order 13. Tricoccæ. — Of this order, which includes the *Euphorbiaceæ* (Spurges), *Buxaceæ* (Box), and *Empetraceæ*, the palæontological history is almost a blank; the first family being unknown in a fossil state, the second dating from the Pliocene, and the third from the Pleistocene.

Order 14. Umbellifloræ. — The occurrence of the typical family *Umbelliferæ*, of which Parsley is a well-known representative, in a fossil state is doubtful, but the other two families are commonly represented. Thus in the *Araliaceæ Panax* occurs in the Miocene, and has also been recorded from the Upper Cretaceous; while *Aralia* also dates from the same epoch and was abundant in the Eocene; and *Hedera* (Ivy) is first known from the early period of the Dakota stage. Finally, in the *Cornaceæ* the typical genus *Cornus* (Cornel) together with *Nyssa* make their appearance in the Upper Cretaceous.

Orders 15, Saxifraginæ; 16, Opuntinæ; 17, Passiflorinæ.— Of these three orders the second is totally unknown in a fossil state, while the only trace of the third (Passion-flowers) is afforded by some exceedingly doubtful leaves from the Oligocene. In the first, however, the family *Hamamelidaceæ* is represented in the European Miocene by species of the existing Asiatic genus *Parrotia*, and by the extinct *Hamamelites* of the Lower Eocene of Sézanne, while *Liquidambar* (Sweet-gum) dates from the Cretaceous of Europe and the United States, the Cretaceous species having the leaves with entire margins.

Order 18. Myrtifloræ.—In the *Onograceæ* the well-known genus *Trapa* (Water-chestnut), characterised by its peculiar spiked fruits and now confined to the Old World, makes its first known appearance in the Laramie Cretaceous of the United States, while in Europe it dates from the Upper Eocene (Lower Oligocene). Curiously enough *T. borealis* of the Tertiary of Alaska and the Laramie stage is allied to the existing Oriental *T. bispinosa*, and not to the four-spined European species; the writer has seen specimens from the Pliocene Siwaliks of Perim Island which probably belong to *T. bispinosa*. The family *Halorhagidaceæ* is not known before the Pleistocene; while there is only very doubtful evidence as to the occurrence of the *Combretaceæ*, *Lythrariaceæ*, and *Melastomaceæ* in a fossil state, although plants from the Eocene of Provence have been referred to *Terminalia* (*Combretaceæ*), and the name *Melastomites* has been applied to others from the Westphalian Cretaceous. In the *Myrtaceæ*, however, we have a large number of fossil forms; thus *Myrtus* (Myrtle) dates from the Upper Eocene of Provence, while an apparently allied Cretaceous type has received the name of *Myrtophyllum*. The genus *Metrosideros*, which includes several climbing species, and is now characteristic of the Moluccas and the Australasian region, appears to be represented in Europe from the Cretaceous to the Miocene; while *Eucalyptus* (Gum-tree), of Australia, occurs in the Laramie Cretaceous and the European Tertiaries. Finally, *Callistemophyllum* and *Leptospermites* are extinct European Tertiary types.

Order 19. Thymelinæ.—In the two families *Thymelæaceæ* and *Eleagnaceæ* the Australian genus *Pimelea* has been recorded from the Lower Tertiary of Europe and the United States, while *Daphne* is common in the European Tertiaries. A number of fossil forms have been referred to the large family *Proteaceæ*, but since at least in some cases the determinations are doubtful it will suffice to state that plants dating from the Eocene have been referred to the existing genera *Dryandra*, *Banksia*, *Knightia*, *Lomatia*, *Grevillea*, and *Persoonia*; while as extinct types we have the Cretaceous *Dryandroides*, and the Eocene *Banksites*, *Knightites*, *Embothrites*, *Lomatites*, &c.

Order 20. Rosifloræ.—This important order is not well represented in a fossil state, although in some genera a considerable number of species have been described. In the *Rosaceæ* the genus *Rosa* (Rose) appears to be represented by several Miocene species; while among the *Amygdalaceæ* *Prunus* (Plum) and *Amygdalus* (Almond) certainly date from the Miocene, and are perhaps of earlier origin. In the *Pomaceæ* *Pirus* (Pear) would likewise appear to occur in the Miocene, but the North American Cretaceous plant referred to this genus is probably different; while of other types *Amelianchier* (Medlar) has been recorded from the Tertiary of

Europe and the United States and also from the Laramie. *Cotoneaster* dates from the Eocene of Provence, and *Cratægus* (Thorn) from the Laramie.

Order 21. Leguminosæ.—The large and well-known order of Leguminous plants, in which the fruit is usually in the form of a pod or legume, in which the seeds are placed, is divided into three families, of which the palæontological history is still imperfect. In the *Papilionaceæ*, characterised by their imbricate papilionaceous petals, leaves from the Miocene of Croatia have been referred to the Australian genus *Gastrolobium*, but the determination is very doubtful; and the same remark applies to those described as *Oxylobium*. *Genista* (Broom) has been recorded from the Miocene of Germany; *Cytisus* from several European Miocene deposits; and *Trigonella*, *Indigofera* (Indigo), and *Tephrosia* from the Upper Miocene of Œningen. *Robinia* apparently dates from the Lower Miocene of Germany; while *Colutea* occurs at Œningen, and is also recorded from the Cretaceous of America and Greenland; and *Erythina* is represented in the Croatian Miocene. Passing by some less important forms we may notice that *Dalbergia*, now mainly confined to India, is common in the European Tertiaries, and is also recorded from the Cretaceous; while the American *Drepanocarpus* occurs in the Eocene of Monte Bolca, the Asiatic *Pterocarpus* in the Miocene, and the American *Piscidia* in the Miocene of Croatia. *Micropodium*, *Phascolites*, and *Ervites* are extinct types from the Upper Eocene of Provence; *Palæolobium*, of the European Miocene, being also extinct. Finally, *Cercis* (Judas-tree), now represented by only a few species in the northern hemisphere, of which one occurs in southern Europe, dates from the Laramie Cretaceous, and is abundant in the Tertiaries. In the *Cæsalpiniaceæ* the genus *Gleditschia*, now confined to North America and China, occurs in the European Miocene, while *Cæsalpinia* dates from the Eocene. The Upper Eocene of Provence has yielded an extinct type termed *Cæsalpinites*. The widely spread tropical and subtropical genus *Cassia* makes its first appearance in the Cretaceous of both hemispheres; *Bauhinia* occurs in the Miocene of Croatia and Œningen; and *Ceratonia* and *Copaifera* date from the Eocene. *Hymenæa*, of tropical America, is found in the Cretaceous of France and New Jersey; and the extinct *Podogonium* ranges from the Laramie Cretaceous to the Œningen Miocene. In the third family, or *Mimosaceæ*, *Prosopis* and *Inga* are described from the Eocene of Eubæa; while *Mimosa* and *Acacia* date from the Upper Eocene of Provence. In conclusion we have to mention the extinct genus *Leguminosites* (fig. 1415, *c*), ranging from the Cretaceous to the Miocene, of which the serial position is at present undetermined.

Order 22. Heterophylleæ.—With this order we come to the end of the Choripetalæ. In the *Aristolochiaceæ*, the type genus

Aristolochia, which includes climbing plants, usually having coloured sepals, dates from the Dakota Cretaceous, and also occurs in the European Miocene. The occurrence of fossil representatives of the *Santalaceæ* is open to some doubt; but remains attributed to the genera *Leptomeria*, *Osyris*, and *Santalum* have been described from the European Eocene and Miocene. The alleged occurrence of fossil representatives of the *Rafflesiaceæ* and *Balanophoraceæ* is too doubtful to need mention.

Division B. Sympetalæ.—With this second primary division of the Dicotyledons we reach the last and most specialised group of plants, characterised by the union of the lower part of the petals into a complete tube. These plants are dependent entirely, or to a great extent, upon the aid of insects for their fertilisation, and a large proportion of them are in all probability of comparatively modern origin. The group is frequently termed Gamopetalæ, and is divided into nine orders.

Order 1. Bicornes.—The family *Ericaceæ* is important from the effect which its massed foliage produces upon the landscape of many regions of the globe. Its type genus *Erica* (Heath), which is exclusively Old World, and very characteristic of the Cape, appears to be unknown before the Upper Miocene of Œningen; while *Andromeda* and *Leucothea* date from the Eocene. *Gaultheria* has likewise been traced back to the Eocene, in which period occur the extinct types described as *Andromedites* and *Arbutites*, and also a species referred to the existing genus *Arbutus*. The Rhododendrons, which some writers make the type of a distinct family, are represented by species of the widely-spread genus *Rhododendron* in the Eocene and Miocene, and by *Azalea* in the Miocene of Croatia and elsewhere. In the *Vacciniaceæ*, the type genus *Vaccinium* (Cranberry) is recorded from the Upper Eocene of Provence and higher deposits.

Order 2. Primulinæ.—In this order the subtropical and tropical genus *Myrsine*, the type of the family *Myrsiniaceæ*, is said to date from the Upper Cretaceous, and is well represented in the Eocene of Provence and the higher Tertiaries. *Myrsinites* is an extinct Tertiary type; and we also find in the Tertiary representatives of *Ardisia*, and some other forms of doubtful affinity.

Order 3. Diospyrinæ.—Coriaceous leaves, found in the Upper Cretaceous of Greenland and the United States, and also in the Lower and Middle Tertiaries, have been described under the name of *Sapotites* as being allied to the American and Australian genus *Sapota*, the type of the family *Sapotaceæ*. The existing American genus *Bumelia* occurs in the Green River Eocene of that country, and also in the Eocene of Provence and other Old World Tertiaries. *Achras*, which is likewise now exclusively American, has been described from the Croatian Miocene. In the *Ebenaceæ* the genus

Diospyros (Ebony), now mainly tropical, is represented by a few species in the Dakota and Greenland Cretaceous, is very abundant in the Upper Eocene of Provence, but has almost disappeared from Europe in the Miocene. Finally, in the *Styracaceæ*, the existing Asiatic and American genus *Symplocos* dates from the Lower Eocene of Europe.

Order 4. Contortæ.—In this order the *Gentianaceæ* (Gentians) are unknown before the Pleistocene. In the *Oleaceæ*, which includes most of the European trees belonging to the present division, *Olea* (Olive) makes its appearance in the Eocene of Provence; while the Australian genus *Notelæa* is recorded from the Eocene and Miocene of the Continent; and *Fraxinus* (Ash) occurs as far back as the Laramie Cretaceous. In the *Apocyanaceæ* we may mention *Nerium*, from the European Cretaceous and Tertiary, and *Tabernæmontana*, from the Eocene and Miocene; together with the extinct *Echitonium*, of the Eocene, and *Apocynophyllum*, of the Cretaceous and Tertiary.

Order 5. Tubifloræ.—In the Convolvulaceæ the tropical genus *Parana* occurs in the Upper Miocene of Œningen, and the somewhat older Tertiary of Croatia; while plants from the upper lignites of Winterhafen have been referred to *Convolvulus*. It is very doubtful if the *Asperifoliaceæ* are represented in a fossil condition, while the *Solanaceæ* (Night-shade, Potato, Tomato, Tobacco, &c.), are unknown.[1]

Order 6. Labiatifloræ.—The only family of this order of which we have any certain palæontological record is that of the *Bignoniaceæ*, in which we have representatives of the existing American genus *Catalpa* in the Laramie Cretaceous, and perhaps in the European Tertiaries. The occurrence of *Bignonia* in the latter is very doubtful.

Order 7. Campanulinæ.—This group, containing the Campanulas, Gourds, &c., seems to be unknown before the present epoch.

Order 8. Rubiinæ.—In this order the *Rubiaceæ* are represented in the Miocene of Bonn by the extinct *Rubiacites;* and we have evidence of the existence of the handsome Asiatic and African genus *Gardenia* in the Miocene of Œningen and the Lower Eocene of the Soissonais. In the *Caprifoliaceæ*, the widely-spread genus *Viburnum* is represented by a number of species in the Laramie Cretaceous, and less commonly in the Tertiaries. The Miocene of Œningen has yielded remains of *Lonicera*.

Suborder 8. Aggregatæ.—With the specialised *Compositæ* we come to the end of our brief survey of the palæontological history of the Vegetable Kingdom. These plants are characterised by the

[1] The Eocene *Solanites* does not belong to this family.

collection of the small separate flowers in a common receptacle, the peripheral florets being modified into strap-like rays surrounding the fertile flowers of the disk. All the fossil forms have been referred to extinct genera, and include *Parthenites* and *Cypselites*, of the Upper Eocene of Provence; *Bidentites*, from the Upper Miocene of Œningen; *Hyoserites*, from the Tertiary of Priesen; *Hieracites*, from Provence; and *Silphidium*, from the Tertiary of Chiavon, which is supposed to be allied to the existing *Silphium*.

In this place it may be well to mention certain flowers from the Amboy Clays of New Jersey—the equivalents of the Dakota Cretaceous—which have been described under the name of *Palæanthus*, and are stated to present resemblances to those of the *Compositæ*. Dr Newberry observes, however, that "though these flowers so much resemble those of the *Compositæ*, we are not yet warranted in asserting that such is certainly their character."

LITERATURE.

The subjoined list comprises only a very limited selection from the great series of works and memoirs dealing with the subject of Palæobotany. The student desirous of fuller information as to the sources of knowledge as to fossil plants should consult the "Literaturverzeichniss" given by Count Solms-Laubach in his "Einleitung in die Paläophytologie" and the complete bibliography of works treating of Palæozoic plants given by Mr Kidston in his "Catalogue of the Palæozoic Plants in the British Museum."

1. "Handbuch der Palæontologie." K. A. von Zittel. Abtheil. ii. "Palæophytologie," by W. Ph. Schimper and A. Schenk. 1879-1889.
2. "Einleitung in die Paläophytologie." Count Solms-Laubach. 1887.
3. "Traité de Paléontologie Végétale." W. Ph. Schimper. 1869-74.
4. "The Geological History of Plants" ('International Scientific Series'). J. W. Dawson. 1888.
5. "Cours de Botanique Fossile." Renault. 1881-85.
6. "Évolution du Règne Végétal." 'Cryptogams,' 1881. 'Phanerogams,' 1885. Saporta and Marion.
7. "Versuch einer Geschichte der Pflanzenwelt." Unger. 1852.
8. "Monographie der fossilen Coniferen. Göppert. 1850.
9. "Die Flora des Bernsteins." Göppert and Menge. 1883.
10. "Flora tertiaria Helvetiæ." O. Heer. 1855-56.
11. "Flora fossilis arctica." O. Heer. 1868-83.
12. "The Fossil Flora of Great Britain." Lindley and Hutton. 1831-37.
13. "The Fossil Flora of the Gondwana System." 'Palæontologia Indica.' Ser. ii., xi., xii. 1863-82. Ottokar Feistmantel.
(*For other works by this author see Kidston's "Catalogue."*)
14. "Die Tertiärfloren der Oesterreichischen Monarchie." 'Abhandl. d. k. k. Reichsanstalt zu Wein.' 1855. C. von Ettingshausen.
15. "On the Fossil Flora of New Zealand." 'Geol. Mag.' 1877. Also "On the Tertiary Flora of Australia." *Ibid.* C. von Ettingshausen.
16. "Acadian Geology," 2d ed. 1868. J. W. Dawson.

17. "The Fossil Plants of the Devonian and Upper Silurian Formations of Canada." 'Mem. Geol. Survey of Canada.' 1871 and 1872. J. W. Dawson.
18. "Report on the Fossil Plants of the Lower Carboniferous and Millstone Grit Formations of Canada." 'Mem. Geol. Survey of Canada.' 1873. J. W. Dawson.
19. "Description of the Coal Flora of the Carboniferous Formation in Pennsylvania and throughout the United States." 'Reports of the 2d Geolog. Survey of Pennsylvania.' 1880 and 1884. L. Lesquereux.
20. "The Tertiary Flora of the Western Territories." 'Reports of the U.S. Geol. Survey of the Territories,' vol. vii., 1878. L. Lesquereux.
21. "Synopsis of the Fauna of the Laramie Group." 'Sixth Ann. Rep. of the U.S. Geol. Survey.' 1885. L. F. Ward.
22. "Flore Carbonifère du department de la Loire et du centre de la France." Grand' Eury. 1877.
23. "Die Versteinerungen der Steinkohlenformation in Sachsen." Geinitz. 1853.
24. "On the Organisation of the Fossil Plants of the Coal-Measures." 'Phil. Trans.,' 1871, 1872, 1873, 1874, 1876, 1877, 1878, 1880, 1881, 1883. W. C. Williamson.
25. "A Monograph on the Morphology and Histology of Stigmaria ficoides." 'Palæontographical Society.' 1887. W. C. Williamson.
26. "On Fossil Cycadean Stems from the Secondary Rocks of Britain." 'Trans. Linn. Soc.' 1868. W. Carruthers.
27. "On the History, Histological Structure, and Affinities of Nematophycus Logani, Carr. (Prototaxites Logani, Dawson), an Alga of Devonian Age." 'Monthly Microscopical Journ.' 1872. W. Carruthers.
28. "Catalogue of the Palæozoic Plants in the British Museum." 1886. R. Kidston.
29. "On the Fructification and Affinities of Archæopteris hibernica." 'Ann. and Mag. Nat. Hist.' 1888. R. Kidston.
30. "A Monograph of the British Eocene Flora." 'Palæontographical Society.' Vol. i. "Filices" (1879, 1880, and 1882), by J. S. Gardner and C. von Ettingshausen. Vol. ii. "Gymnospermæ" (1883, 1884, and 1885), by J. S. Gardner.
31. "On Mesozoic Angiosperms." 'Geol. Magazine.' 1886. J. S. Gardner.
32. "The Appearance and Development of Dicotyledons in Time." *Ibid.* 1887. J. S. Gardner.
33. "Observations sur les Algues calcaires appartenant au groupe des Siphonées verticillées et confondues avec les Foraminiféres." 'Comptes rendus,' tom. lxxxv., 1877. Munier-Chalmas.
34. "Die Sogenannten Nulliporen" (Lithothamnium und Dactylopora). 'Abhandl. der k. Bayerischen Akad. der Wiss.' Bd. XI. 1874.
35. "Zur Kenntniss fossiler Kalkalgen (Siphoneen)." 'Neues Jahrb. für Min. Geol. und Palæontologie.' 1880. Steinmann.
36. "Geologische Algenstudien." 'Jahrb. d. k. preuss. geol. Landesanstalt.' 1880. Bornemann.
37. "On the Fossil Flora of the Radstock Series of the Somerset and Bristol Coalfield." 'Trans. Roy. Soc. Edin.,' vol. xxxiii. 1888. A. C. Seward.
38. "Sketch of Palæobotany." 'Fifth Ann. Rep. of the U.S. Geol. Survey.' 1885. L. F. Ward.

APPENDIX

APPENDIX.

I. INVERTEBRATE ANIMALS.

Foraminifera.

Mr E. Wethered has shown ('Geol. Mag.,' May 1889) that forms of *Girvanella* (see p. 127) occur abundantly in some of the Jurassic limestones of Britain. Mr Wethered has also made the interesting observation that the spheres of some of the so-called "pisolites" of the Jurassic series are in reality formed by the growth of layers of *Girvanella* round a central nucleus, and are, therefore, not of the nature of ordinary oolitic grains.

Receptaculitidæ (p. 170).

The remarkable fossils which are grouped together under the name of *Receptaculitidæ* have recently formed the subject of an important investigation by Herr Rauff ('Zeitschr. d. Deutschen Geol. Gesellschaft,' Bd. XL.) The following are the principal general conclusions at which this observer has arrived:—

1. The *Receptaculitidæ* are spherical or pyriform bodies, with a central closed cavity, the supposed basin-shaped examples being only fragments of the base.

2. Each of the individual spicular elements forming the wall of the body is composed of six parts—viz., an external plate of an essentially rhombic form, four diagonally intersecting tangential arms which lie immediately below the outer plate, and a radial arm or pillar which springs from the centre of the outer plate on its inner side, and is directed perpendicularly inwards.

3. An upper and lower pole may be distinguished on the exterior

surface, the arrangement of the plates at these points being peculiar. The basal pole (the starting-point of growth) is constituted by a circle of eight (or four) plates. The apical pole is closed by a variable, but always large, number of plates.

4. Each of the five arms of the skeletal elements or spicules is traversed by an axial canal, the canals of the four tangential arms having a conspicuously fusiform shape.

5. The radial arms or pillars terminate on the inner or "gastral" side in a conical dilatation, which is laterally extended till adjoining pillars touch. This internal thickening of the radial pillars is not furnished with a special plate, corresponding with the external plate, and is not penetrated by transverse canals.

6. The inner or "gastral" wall of the fossil is imperforate, the pores described by Billings being the result of fossilisation.

7. The genus *Ischadites* agrees essentially with *Receptaculites* in structure, but its skeletal elements are more slender. An apical aperture is in some cases clearly wanting in *Ischadites*, and probably did not exist at all.

8. The genus *Acanthochonia* is identical with *Ischadites*.

9. The geological range of *Ischadites* extends to the Upper Devonian.

10. The genus *Polygonosphærites* (*Sphærospongia*) is similarly constructed to *Receptaculites* as regards the tangential arms of the spicules, but the radial arms or pillars are wanting.

11. The *Receptaculitidæ* are not *siliceous* organisms, but the skeleton was originally *calcareous*, and the siliceous examples are the result of silicification. The group, therefore, cannot be referred to the Hexactinellid Sponges, and its systematic position is still entirely uncertain.

Mastopora and Cyclocrinus (p. 186).

In the memoir just referred to, Herr Rauff expresses the opinion that the genera *Mastopora* (*Nidulites*) and *Cyclocrinus* have no relationships with the *Receptaculitidæ*, but that they appear to be related to the *Polyzoa*.

Calcispongiæ (p. 178).

Some interesting discoveries as to the occurrence of Mesozoic Sponges have recently been made by Dr George J. Hinde, who has been good enough to furnish the following note of his investigations on this point: "In the Middle Lias of Northamptonshire (zone of *Ammonites spinatus*) some very minute Calcisponges have been lately discovered, with the same delicate structural characters as in the existing family of the *Leucones*, Haeckel, and they have even

been placed in the recent genus *Leucandra*, Haeckel. The largest of these fossil sponges is under 4 mm., or about one-sixth of an inch in height, and the spicules in their walls are as perfect as in recent specimens. A remarkable assemblage of small Calcisponges has also been discovered by Mr Walford in the Inferior Oolite (zone of *Ammonites Parkinsoni*) of Dorset. In their diminutive proportions they resemble living Calcisponges, but they all possess a structure of solid fibres, characteristic of *Pharetrones*. They mostly belong to the genera *Eudea*, *Peronella*, *Blastinia*, and to a new genus not yet described. Calcisponges of larger dimensions, belonging to *Peronella* and *Lymnorea*, are also abundant in the Inferior Oolite of Cheltenham. Certain zones of the Great Oolite in the neighbourhood of Bath are very rich in Calcisponges, principally of the genus *Peronella*. Higher up in the Oolitic series there is a well-marked zone of Calcisponges in the Lower Coral Rag of Yorkshire. They have mostly been hitherto placed in *Stellispongia*; species of *Peronella* and *Blastinia* are also present."

STROMATOPOROIDEA (p. 229).

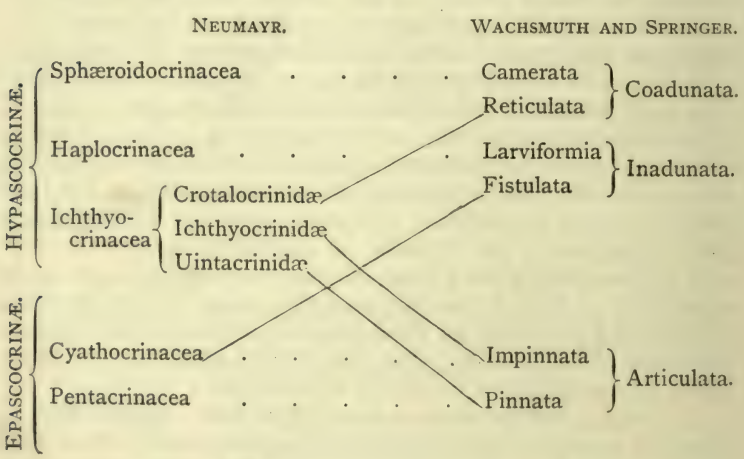
Since the earlier portion of the present work was written, the author has had the opportunity of studying the fasciculus of Dr Waagen's Monograph on the "Salt Range Fossils," which deals with the *Hydrozoa* ('Palæontologia Indica,' Ser. XII., No. 7, 1877). The most important point brought out in this memoir is, that the "Productus Limestone" of the Salt Range of India, the age of which is Permo-Carboniferous, contains various *Hydrozoa* which are more or less closely related to *Stromatopora* proper. For these the new genera *Disjectopora*, *Circopora*, *Carterina*, and *Irregulatopora* are proposed; but it would be impossible to make the structure of these intelligible without illustrations. It may, however, be considered as proved that the geological range of the Stromatoporoids, as a group, has by these researches been extended into the beginning of the Permian period; the latest undoubted types of the group previously known being Upper Devonian.

Dr Waagen, further, deals at some length with the general structure and zoological affinities of the Stromatoporoids. He divides them into two families, and refers them to the *Hydrocorallinæ*. It is unnecessary, however, to discuss Dr Waagen's views on these subjects here; since the conclusions which he has reached would probably have been more or less modified had he been acquainted with the previously published "Monograph on the British Stromatoporoids" (Palæontographical Society, 1885) by the present writer, in the general introduction to which the same questions have been dealt with in considerable detail.

Classification of the Crinoidea (p. 445).

Dr P. Herbert Carpenter has kindly supplied the author with the following note as to the classification of the Crinoids proposed by Neumayr in his recently published important work "Die Stämme des Thierreichs": "The new classification of the *Crinoidea* proposed by Neumayr is primarily based upon the condition of the mouth and ambulacra. These are either subtegminal (*Hypascocrinæ*) or free and exposed upon the ventral surface (*Epascocrinæ*). The first-named group includes all the Palæocrinoids, except *Cyathocrinus* and its allies (Families 12–20), which have been already distinguished as *Fistulata* by Wachsmuth and Springer. It has also been shown by these authors that some of the *Ichthyocrinidæ*, at any rate, had an exposed mouth and open ambulacra (see p. 431); so that this family can find no place in the *Hypascocrinæ*. Except, too, for having a subtegminal mouth, the *Haplocrinidæ* and their allies (*Larviformia*) seem to be more closely allied to the *Fistulata* than to the other Palæocrinoids (*Camerata*)."

The general relations of Neumayr's classification to that proposed by Wachsmuth and Springer may be seen in the following table:—



Cystoidea (p. 447).

An important posthumous work by M. Joachim Barrande on the Cystideans of Bohemia has recently been published, and Dr P. Herbert Carpenter has been good enough to furnish the author with the following note as to its contents:—

"This elaborate work contains descriptions of a large number

of new Cystideans from the Lower Palæozoic rocks of Bohemia. Some valuable morphological observations are also recorded therein; but most of them refer to questions of too complex a nature for discussion here. One point, however, must be noticed. In the new genus *Aristocystites* and in some half-dozen others Barrande describes the calcareous plates of the test as covered by a smooth 'external epidermis' which completely closes the openings of the pore-canals that penetrate the substance of the plates. This epidermis is very thin, not more than $\frac{1}{100}$ part of an inch in *Proteocystites*, and is therefore but rarely preserved to any great extent. The pores are sometimes isolated (haplopores), or a pair may be linked by a horse-shoe-shaped groove, or open together in a small oval depression, the 'oscule,' the whole structure being commonly known as a 'diplopore.' It was the resemblance of these diplopores to the groups of twin ambulacral pores in the Ordovician Sea-Urchin *Bothriocidaris*, which led Lovén to point out that the old theory of the connection of the diplopores of the Cystideans with the ambulacral system might after all be correct. This view, however, will have to be abandoned altogether if the pores really are closed by the external epidermis in the manner described by Barrande. But there is some doubt as to whether the appearances described by him may not be capable of a different interpretation, more especially as he suggests in one place that the pores may have been connected with tube-feet like those of the Urchins, while in another he notices their similarity to the respiratory pores of the Asterids which give passage to the gills or papulæ. But neither of these explanations could be possible if the pores really are closed as he describes.

"Neumayr, believing Müller's classification of the Cystidea according to the characters of their pores to be no longer a practicable one, has recently proposed the following scheme, which may be adopted until a fuller morphological knowledge of the group has provided us with the materials for a better one.

"I. Order Sphæronitidæ.—Test composed of numerous irregularly disposed plates, which may be aporous or bear haplopores or diplopores, but never rhombs. Five ambulacra, sometimes terminating in feebly developed arms. Generally sessile, but sometimes free or stalked.

"*Family* 1. *Sphæronitinæ.*—Ambulacra superficial and branching. *Sphæronites*, *Glyptosphærites*, *Eucystis*, *Proteocystites*, *Protocrinus.*

"*Family* 2. *Aristocystinæ.* Ambulacra subtegminal and branching. *Aristocystites*, *Pyrocystites*, *Craterina.*

"*Family* 3. *Mesitinæ.* Ambulacra superficial and simple. *Mesites*, *Agelacrinus*, *Edrioaster*, *Cytaster*, *Hemicystites.*

"II. Order Echinosphæritidæ.—Test composed of numerous rhombiferous plates; often with only three ambulacra, and slightly

developed arms. Sessile or stalked. *Echinosphærites*, *Dendrocystites*, *Caryocystites*, *Arachnocystites*.

"III. Order Pleurocystidæ.—Test shortly stalked and asymmetrical, the plates of the two sides being differently arranged except in the oldest genera (*Trochocystites*). Arms few and small. *Pleurocystites*, *Ateleocystites*, *Balanocystites*, *Mitrocystites*.

"The above scheme takes no account of such types as *Caryocrinus*, *Porocrinus*, *Echinoencrinus*, *Lepadocrinus*, *Callocystites*, and several other forms in which the plates of the test are few in number, with a more or less regular arrangement as in the Crinoids; while in *Cystoblastus* and *Asteroblastus* there is a calyx very similar to that of the Blastoidea. Most of these genera have hydrospires, either generally distributed on the calyx plates (*Caryocrinus*), or limited to a few of them as in *Echinoencrinus*, while *Asteroblastus* has diplopores.

"As at present constituted the class of the Cystidea is an extremely heterogeneous one, and much further investigation will be necessary before anything like a natural classification of the group becomes at all possible."

Bactrites (p. 846).

According to the observations of Branco ('Zeitschr. d. Deutschen Geol. Gesellschaft,' Bd. XXXVII., 1885), the initial chamber of the shell of *Bactrites* is an ovoid and dilated sac, similar to that of the shell of the Ammonoids and of *Spirula*. The genus *Bactrites* must therefore be removed to the *Ammonoidea*. According to the views of Branco, the genus should be ranked with the *Goniatitidæ*, the particular group of these to which it is referable occupying an intermediate position, as regards the form of the initial chamber, between the *Ammonitidæ* and the *Belemnitidæ*.

II. VERTEBRATA.

Pisces.

Chimeroidei.—As is mentioned in the Addenda, Mr Smith Woodward has recently made the genus *Myriacanthus* (p. 951) the type of the family *Myriacanthidæ*, which is defined as follows: Body elongated; anterior dorsal fin placed above the pectoral, and furnished with a long, straight spine. Teeth forming two or three pairs of thin dental plates in the upper jaw, the hinder pair alternated and not closely approximated in the middle line; lower teeth consisting of a pair of large dental plates meeting at the symphysis, and a median incisor-like tooth in front. A few dermal plates on the head; and a long prehensile spine upon the muzzle of the male.

Incertæ sedis.—Remains of a fish from the Oxford Clay of Peterborough have been described as *Leedsichthys*,[1] which apparently indicates the largest Jurassic representative of the class, although its serial position cannot yet be determined. A bone which is regarded as the frontal has a length of 24 inches, while the squamous hyomandibular is at least 15 inches long. The most remarkable features of this fish are, however, shown in the pectoral fin-rays, which sometimes attain a length of 5 feet, and frequently branch in a forked manner, but are not jointed. Each ray consists of fibrous bone, and appears to be composed of a number of long and tapering splints which are incompletely fused together, and the two halves of the ray remain separate.

Reptilia.

Anomodontia.—The author's recent study of the Anomodont remains in the British Museum has enabled him to make some amendments on the characters of the families and genera given in the text.

In *Tapinocephalus* (pp. 1057-58) the dentition, although it may have been of a carnivorous type, was not differentiated into incisives, tusks, and cheek-teeth; and it is highly probable that there were no secondary nares. It does not appear by any means certain that the one tooth on which the genus *Glaridodon* (p. 1061) is founded, is really distinct from *Titanosuchus* (p. 1058).

In the *Galesauridæ* (pp. 1058-59) the single narial aperture of the type specimen of *Ælurosaurus* is due to imperfection; and it is probable that the same is the case with *Cynodraco*, *Cynochampsa*, and *Cynosuchus*.[2] The latter has 7 or 8 cheek-teeth, with a posterior basal cusp, but the incisive and cheek-teeth appear to have no serrations on the posterior edge. *Cynochampsa* was probably allied, having $\frac{4}{3}$ incisive teeth as in *Cynosuchus*. In *Cynodraco* and the type of *Ælurosaurus* there are $\frac{5}{4}$ incisive teeth; and the crowns of the incisive and cheek-teeth have serrated posterior edges; and it has yet to be proved that *Ælurosaurus* is generically distinct from *Cynodraco*. In *Tigrisuchus* there are three pairs of upper incisive teeth.

Gorgonops (p. 1059) differs from the *Galesauridæ* in having the temporal fossæ roofed over, and apparently in the absence of second-

[1] The practice of making such barbarous compounds as *Leedsichthys*, *Owenia-suchus* (p. 1191), and *Wardichthys* (p. 979), is much to be deprecated. If a change be permissible, the terms *Leedsia* and *Wardia* may be suggested in place of the first and third of these uncouth names.

[2] By an error (see Corrigenda) these three genera are stated to have double nares, while in *Tigrisuchus* the nares are said to be single.

ary posterior nares. Roofed temporal fossæ also occur in the American genus *Chilonyx* (p. 1060); so that both of these forms approximate in this respect to the Pariasauria, although distinguished from the typical representatives of that group by the absence of sculpture on the cranial bones. *Gorgonops* may be regarded as the type of the family *Gorgonopidæ*, with an uncertain serial position.

The genus *Embolophorus* (p. 1060) is the only one in which the articulation of the capitula of the ribs to the intercentra has yet been observed.

It appears that there is no justification for Eichwald's reference of the tooth represented in fig. 983 (p. 1062) to *Deuterosaurus* rather than to *Brithopus;* the former genus having been founded upon part of the vertebral column of a smaller reptile than the one to which the humerus of *Brithopus* belonged.

The vertebræ of the *Diadectidæ* (p. 1061) are distinguished by the presence of zygosphenal (hyposphenal) articulations; while the skull has no secondary posterior nares. *Empedias* differs from *Diadectes* by the absence of a tusk; while *Helodectes* is distinguished from both by the double row of cheek-teeth.

Sauropterygia.—It is stated on page 1077 that the genus *Cimoliosaurus* has no trace of an interclavicle; it has, however, been subsequently suggested that certain splint-like bones found with some skeletons of the Oxfordian representatives of this genus are really the last remnants of the interclavicle and clavicles; the interclavicle probably fitting into the notch shown between the ventral plates of the scapulæ in fig. 988 (p. 1069).

Chelonia.—In a recent paper Dr Baur states that in the skull of *Protostega* (p. 1089) the parietals were connected by vertical plates with the pterygoids, and he accordingly regards the *Protostegidæ* as less specialised than the *Dermochelyidæ*. If this reference be correct there will be evidence of a nearer affinity between the Athecata and Testudinata than has hitherto been supposed.

The same writer also doubts the Chelonian nature of the problematical *Psephoderma* (p. 1089), and suggests that it may be founded upon the dermal armour of *Nothosaurus*. This argument is supported by the absence of Chelonian bones in the Lettenkohle (Lower Keuper), where *Psephoderma* is not uncommon; but the absence of a dermal armour in the *Lariosauridæ*, so far as it goes, is against this view.

In the *Testudinidæ* the genus *Palæochelys* (p. 1108), as is well shown by a specimen from the Pliocene of Italy recently described as *Emys Portisi*, has some of the neural bones tetragonal and others octagonal, and is thereby more nearly allied to *Nicoria* and the land tortoises than to *Ocadia*. The so-called *Emys crassa*, of the Upper Eocene of Hampshire, is, therefore, referable to *Ocadia*.

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[1] = *Leptodactylidæ*. See Corrigenda.

[2] = *Xenopodidæ*. See Corrigenda.

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[1] *Limnotherium* in text. See Corrigenda.

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[1] *Errore Saurinichthys.* See Corrigenda.

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